SPATIAL EFFECTS IN RELATION TO REPRODUCTIVE PERFORMANCE OF COMMON MURRES *URIA AALGE* AT A RE-ESTABLISHED COLONY

GERARD J. MCCHESNEY[1*], JULIE L. YEE[2], MICHAEL W. PARKER[1,6], WILLIAM M. PERRY[3], HARRY R. CARTER[4†], RICHARD T. GOLIGHTLY[4] & STEPHEN W. KRESS[5]

[1]*US Fish and Wildlife Service, San Francisco Bay National Wildlife Refuge Complex, Fremont, California 94555, USA*
[*](gerry_mcchesney@fws.gov)
[2]*US Geological Survey, Western Ecological Research Center, Santa Cruz Field Station, 2885 Mission St., Santa Cruz, California 95060, USA*
[3]*US Geological Survey, Western Ecological Research Center, Dixon Field Station, 800 Business Park Dr., Dixon, California 95620, USA*
[4]*Humboldt State University, Department of Wildlife, 1 Harpst St., Arcata, California 95521, USA*
[5]*Audubon Seabird Institute, 12 Audubon Rd., Bremen, Maine 04551, USA*
[6]*Current Address: California Institute of Environmental Studies, P.O. Box 1185, Davis, California 95617, USA*
[†]*Deceased*

ABSTRACT

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A main goal of seabird colony restoration is for the colony to become self-sustaining. To do so, elevated rates must be attained in (1) reproductive success and (2) recruitment by immigrants and birds produced at the colony. Thus, an understanding of the factors affecting reproductive success and recruitment at restoration sites is vital. We examined how spatial features at the colony level affected reproductive success of Common Murres *Uria aalge* (hereafter, murres) over a six-year period at Devil's Slide Rock, California, a colony re-established using social attraction techniques. Clusters of sites with similar egg-laying dates, as well as high hatching and breeding success, occurred in the densest portion of the colony, which was also the last area occupied by murres at the time of extirpation and the first area to be re-colonized. Clusters of sites with low success occurred in outlying, low-density portions of the colony. Breeding success, influenced largely by high fledging success, averaged > 60% most years. Reproductive success was greatest at breeding sites with earlier egg-laying dates, those in closest proximity to the breeding sites of other murres and the Brandt's Cormorant *Urile penicillatus*, and those outside Brown Pelican *Pelecanus occidentalis* disturbance zones. Based on our findings, for future murre restoration projects in the California Current System, we suggest (1) placing social attraction equipment in the area(s) last utilized by murres prior to extirpation, (2) attempting to establish two dense breeding groups, (3) targeting sites already utilized regularly by nesting Brandt's Cormorants, and (4) avoiding sites or habitats prone to disturbance by larger and aggressive species such as Brown Pelicans, Bald Eagles *Haliaeetus leucocephalus*, or Common Ravens *Corvus corax*.

Key words: Common Murre, *Uria aalge*, reproductive performance, spatial effects, colonial breeding, re-colonization, social attraction

INTRODUCTION

Conservation of seabirds has been practiced widely over the past century, mainly by reducing or preventing human disturbance at breeding colonies, removing invasive predators (e.g., cats *Felis catus*, rats *Rattus* spp., gulls *Larus* spp., corvids *Corvus* spp.) from colony areas, reducing or preventing mortality factors away from colonies (e.g., gill nets, longlines, oil spills, etc.), or enhancing nesting habitats at colonies (e.g., removing or re-establishing vegetation; Jones & Kress 2012). The latter practice often occurs under the assumption that populations exist nearby and that individuals will expand or re-occupy improved habitats within years of the initiation of restoration actions. Some seabirds have also benefited when altered fishery extractions provide more food, e.g., Common Murres *Uria aalge* in the California Current and elsewhere (Ainley *et al.* 2021). However, additional efforts to re-establish specific seabird colonies have been developed that use social attraction and focus on (1) attracting adults to unused, abandoned, or artificial breeding habitats; (2) translocating chicks to unused breeding habitats in hopes that they will return to breed; or (3) a combination of these methods (Kress & Nettleship 1988, Kress 1998, Jones & Kress 2012). Although the

progress of many social attraction projects is monitored intensively— often measured by the numbers of breeding birds, reproductive success, or behavior (Kappes *et al.* 2011)—within-colony spatial factors that facilitate progress are rarely considered. Colony growth for long-term success of a restoration project can be dramatically altered if birds who experience low breeding success abandon the target location, low reproductive success discourages prospective immigrants, or the colony does not produce enough young for future recruitment (Danchin *et al.* 1998).

Common Murres (hereafter, murres) breed colonially on rocks, islands, and cliffs along the coasts of the North Atlantic and North Pacific oceans (Ainley *et al.* 2021). Several studies have examined spatial features affecting reproductive success in murres (including Common and Thick-billed murres [*Uria lomvia*]), mainly where they breed on cliff ledges of varying length and width (Birkhead 1977, Gaston & Nettleship 1981, Birkhead *et al.* 1985, Hatchwell 1991, Gaston & Elliott 1996, Harris *et al.* 1997). Both species breed in dense clusters, with neighboring adults often touching one another. Murres do not build nests, laying their single eggs directly on the ground but keeping them in their brood pouch when

incubating (Ainley *et al*. 2021). Factors known to be associated with greater reproductive success include greater numbers of adjacent and nearby neighbors (i.e., density), presence of rock walls adjacent to breeding sites, and greater width of breeding ledges. In certain cases, slope is also a significant success factor, with sites that are more level experiencing greater success than those on steeper grades (Gaston & Nettleship 1981, Birkhead *et al*. 1985, Harris *et al*. 1997). At the Isle of May, Scotland, Harris *et al*. (1997) also documented a positive relationship between vertical distance to the cliff top and reproductive success. In addition to these habitat features, timing of breeding can be important. Murres that lay eggs more synchronously with the overall colony (i.e., near peak egg-laying; Hatchwell 1991) or with an adjacent neighbor (Murphy & Schauer 1996) have higher breeding success than those out of synchrony. Further, earlier breeders tend to have higher breeding success than later breeders within the same group (Wanless & Harris 1988, Boekelheide *et al*. 1990b).

Along the central California coast, we used social attraction techniques (decoys, mirrors, and sound recordings) to re-establish an extirpated murre colony on a small sea stack called Devil's Slide Rock (DSR; Carter *et al*. 2003a, Parker *et al*. 2007). DSR held close to 1 500 breeding pairs before it was extirpated as a breeding colony in the short period between 1982 and 1986, mainly as a result of gill-net and oil spill mortality (Takekawa *et al*. 1990; Carter *et al*. 2001, 2003a). After a 10-yr absence of breeding murres, six pairs re-established breeding during the first year (1996) of restoration efforts. In that year, decoys had a significant effect on where birds attended and recruited. Individual murres more frequently attended low-density plots and aisles among decoy plots, while larger groups frequented high-density plots (Parker *et al*. 2007). Murre densities were significantly greater near mirrors (< 30 cm); indeed, five of six breeding sites were within 60 cm of a mirror. In 1996–1998, all murre breeding occurred within the same small portion of the eastern side of the rock that had substantial murre attendance in 1986–1987 (shortly after breeding ceased) and occasional murre attendance from 1988 to 1994, with Parker *et al*. (2007) suggesting that this area represented high-quality habitat (Parker *et al*. 2007). In 1999, the colony began to increase further (70 breeding pairs) and expanded onto the western side of the rock. By 2004, the colony increased to 190 breeding pairs. Because of increasing population size and high breeding success, social attraction techniques were altered during 2000–2005 by reducing or increasing local numbers of decoys to encourage birds to recruit within established breeding clusters; also, decoys were placed in locations of certain Brandt's Cormorant *Urile penicillatus* nests to protect neighboring murres from being usurped by the larger cormorants.

As the DSR colony grew larger, the influence of social attraction equipment became less clear. Therefore, our objective in the present study was to better understand the factors influencing restoration progress by examining how the spatial features of the colony were affecting murre reproductive activity and success. Murre breeding habitat on DSR differs from most other colonies studied for habitat effects in that breeding is concentrated on the gently-sloped top of the rock rather than the ledges of steep cliffs. We tested the hypotheses that (1) timing of egg-laying and reproductive success at individual breeding sites is correlated with timing of egg-laying and success at neighboring breeding sites, and (2) reproductive success is related to spatially explicit conditions such as density or proximity of neighboring breeding sites, threats (e.g., pelican presence), attractants (e.g., mirrors or decoys), and topographic attributes

(e.g., slope or rock wall). We also analyzed how egg-laying dates and reproductive success varied across years, from 2000 to 2005, the last years in which social attraction techniques were employed. Specifically, we developed a geographic information system (GIS) layer of attributes on DSR for each year from 2000 through 2005. This information may help guide future management actions, assist with designing other restoration projects, and help to better understand factors influencing successful colony re-establishment and subsequent colony growth by murres.

STUDY AREA

DSR (37.58°N, 122.52°W) is a small 22-m-high sea stack located ~300 m from the mainland, just south of San Francisco, California. The relatively gentle sloping-to-flat top portion of the rock consists of ~200 m^2 of vegetation-free granitic substrate. As seen in aerial photographs, most of this area was nearly covered by breeding murres in 1979–1982, just prior to human-caused colony extirpation (Takekawa *et al*. 1990). During the study period, in addition to breeding murres, DSR was used by up to 92 breeding pairs of Brandt's Cormorants, two to three nesting pairs of Western Gulls *Larus occidentalis*, and roosting seabirds of several species. The rock is part of the California Coastal National Monument managed by the US Bureau of Land Management.

METHODS

Social attraction techniques

The social attraction effort included murre decoys, sound systems playing recorded murre calls, and three-sided mirror boxes. In 1996–1998, 384 life-sized murre decoys (288 standing posture and 96 incubating posture) were placed in 12 decoy plots and four control plots. Each plot measured ~100 cm by 170 cm and was on gently-sloped (< 10°) terrain with a vertical rock wall (> 5 cm high) at one edge of the plot. One three-sided mirror box was placed on the edge of each decoy plot. Not directly associated with plots, two identical but independent audio systems (compact disc player, amplifier, and speakers) played murre calls. Four speakers were arranged at regular intervals along the top ridge of the rock. Audio systems were powered by two 60-watt photovoltaic panels that charged three 12-volt DC deep-cycle gel-cell batteries, and recordings of murre vocalizations were broadcast 24 hr per day (Parker *et al*. 2007).

After the annual cessation of breeding activities, decoys were removed for cleaning and the sound system was turned off. Decoys and sound were redeployed the following winter, two to four months prior to the expected start of the next breeding season. Beginning in 1999, decoy arrangements were modified each year in favor of developing dense, core breeding groups of murres. Decoy plots that were not colonized by murres were removed, while other plots were thinned of decoys to open up breeding space or had small numbers of decoys added to protect breeding murres from competition with larger cormorants. In 2005, decoys were placed only on the eastern portion of the rock to test the efficacy of complete decoy removal. During the winter of 2001–2002, the eastern sound system was lost in a storm and was not replaced. Social attraction methods on DSR ceased following the 2005 season because we ascertained success in the re-establishment. In 2005, a remote-controlled video system, consisting of two cameras and a small communication tower, was placed on the rock to assist in monitoring.

Data collection

We monitored murre reproductive performance from several mainland vantage points using high-powered telescopes. All potential breeding sites on the rock were checked every 1–2 d (often several times per day) from mid-April until all attendance ceased for the season (usually early August). Breeding sites were those at which an egg was laid. Territorial sites were those that were attended by at least one bird on ≥ 15% of observation days but no egg was known to have been laid. Egg-laying date and whether a chick hatched and survived to departure were determined for each breeding site. Because chicks depart the colony with the male parent when they are about one-quarter adult size (Ainley *et al*. 2021), we considered success to have been attained if they reached 15 d of age and were not seen dead or depredated at a later date (following Harris *et al*. 1997).

In August 2000, we located all social attraction equipment, murre breeding and territorial sites, cormorant nest sites, and other important features using a survey grade Trimble 5800 Global Positioning System (GPS) rover with a Trimble Survey Controller (horizontal and vertical accuracy of 0.03 m). Because breeding birds were no longer present, observers positioned on both the rock and mainland worked together, using photographs and sketches of the colony, to pinpoint locations of each murre and cormorant site. Additional points were obtained from potential breeding habitat having no active breeding, based on archived 1979–1982 aerial photographs from studies conducted by Sowls *et al*. (1980) and Briggs *et al*. (1983), a period prior to extirpation of the former murre colony. These data resulted in a GIS layer of all potential murre breeding habitat on the rock, including former habitat not currently used (Fig. 1). In subsequent years, we used GIS maps in combination with both ground-based and aerial photographs taken during the breeding season to locate formerly mapped features and to map new breeding sites, decoys, and other features. GPS data collection was repeated in 2001, 2004, and 2005. Locations of features present in 2002–2003, but not in 2004 or 2005, were digitized from field maps.

Data analysis

We analyzed colony reproductive success at individual breeding sites for six years (2000–2005). We examined three reproductive success parameters: hatching success, i.e., the proportion of eggs that hatched (first eggs only); fledging success, i.e., the proportion of chicks that reached 15 d of age; and breeding success, i.e., the proportion of breeding pairs that successfully produced a 15-d-old chick (including replacement clutches). We numerically coded
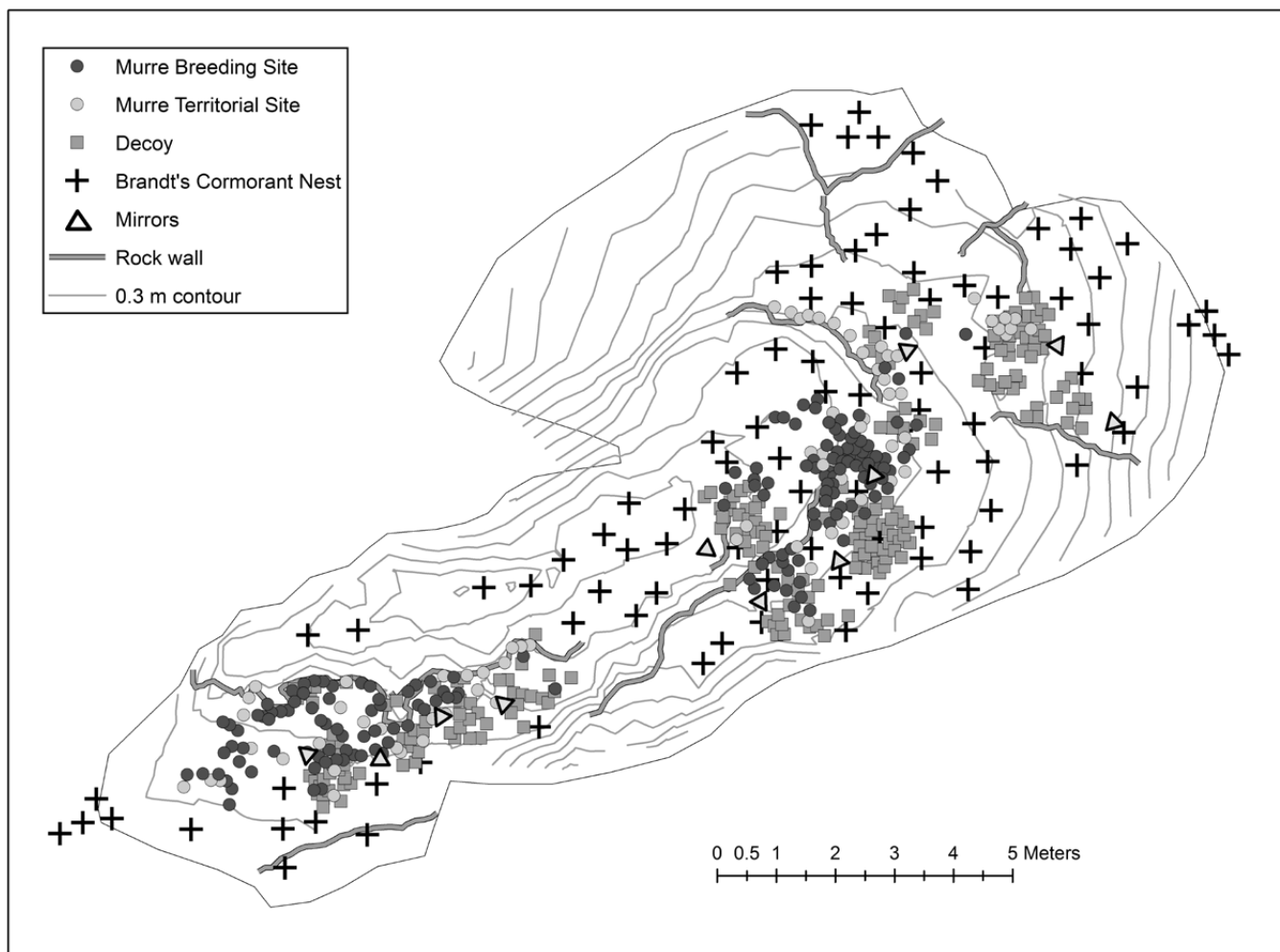

Fig. 1. Map of Devil's Slide Rock, California, USA derived from GIS spatial data. For display purposes, data from only one year are shown for the following: Common Murre *Uria aalge* breeding and territorial sites, 2005; Brandt's Cormorant *Urile penicillatus* nests, 2004; decoys and mirrors, 2000.

reproductive outcomes as one for successes or zero for failures; therefore, success rates were equivalent to outcome means.

Spatial autocorrelation of reproductive success at distances ranging from 0.3 to 12 m was tested using Global Moran's I (ArcGIS® ArcMap™ GIS software). The Getis-Ord General G hot spot analysis was used to map significant clusters of breeding sites having either high or low success rates. Because murre breeding success is often correlated with egg-laying date (Wanless & Harris 1988, Boekelheide *et al*. 1990b, Hatchwell 1991, Shultz *et al*. 2009), we tested for spatial autocorrelation of egg-laying dates with Global Moran's I at distances of 0.3 to 3.0 m in 0.3 m increments; clustering was mapped using a Space Time Intensity model of Getis-Ord General G with a time window of seven days and space window of 0.3 m. We compared the patterns of observed breeding success/egg lay dates relative to the expected pattern under the null hypothesis that successes/dates occurred randomly over the observed breeding site locations. We considered Global Moran's I tests to indicate significant spatial patterns when the *z*-score ($|Z|$) > 1.96, or equivalently $P < 0.05$; specifically, we interpreted $Z > 1.96$ to indicate spatial autocorrelation while $Z < -1.96$ would indicate over-dispersion (i.e., no clustering). Maps of Getis-Ord General G tests indicated clustering of high success rates at sites where $Z > 1.96$ and low rates where $Z < -1.96$.

For murre breeding sites that were highly clustered, we hypothesized that breeding sites benefited from the protection of surrounding murres and that breeding sites positioned near the centers of clusters had higher success rates than those along the edges of clusters or away from clusters. For each breeding site location, we calculated two types of metrics to represent position relative to clusters: (1) the pooled density of breeding and territorial murre sites (sites/m^2) as estimated by the kernel density estimator in ArcMap with a cell size of 0.15 ft (0.046 m) and a 1.5 ft (0.46 m) search radius; and (2) average distance (m) to a given number (range 5–20) of nearest breeding murre neighbors.

Because we did not have prior information on the numbers of neighbors that would be the best predictors for success, for each set of distance variables (murres or cormorants), we fit and compared logistic regression models using different numbers of neighbors. We repeated these comparisons for each of the murre reproductive success parameters (hatching, chick departures, and breeding), included all other covariates in these models to control for their potential effects, and used second order Akaike's Information Criterion (AICc) to select the best number of neighbors (lowest AICc; Burnham & Anderson 2002). We considered models, and the covariates within them, to predict similarly well when their AICc values did not differ by more than two. When two models differed by ΔAICc > 2, we considered the model with the lower AICc value to be the better one.

Similarly, we were interested in the potential effects on reproductive success of other seabird species using the rock (nesting Brandt's Cormorants and roosting Brown Pelicans *Pelecanus occidentalis*), social attraction equipment (decoys and mirrors), murre egg laying dates, and topographical features (degree of slope and rock walls). Cormorant nests and murre decoys were interspersed with murre breeding sites throughout much of the rock, and we calculated average distances between each murre breeding site and the nearest five to 20 decoys and nearest one to five Brandt's Cormorant nests followed by a comparison of AIC to select the best average

distance variable. For the year 2005, when no cormorant nests were present, we substituted a nearest cormorant nest neighbor distance of 18 m, which just exceeds the maximum measured distance (16 m) in years when cormorants nested and is about the width of the breeding habitat. Although a larger distance might be a better physical representation for the absence of cormorants from the rock, we chose a low-value substitution to avoid over-leveraging the statistical effects of distance. Whereas an excessively leveraged distance effect can be confounded with differences in breeding between 2005 and other seasons, the only risk of an under-leveraged distance effect is that the effect may be underestimated.

For each year, we geographically zoned areas adjacent to rock walls, adjacent to mirrors, and within Brown Pelican roosting areas, and we identified murre egg-laying sites as inside or outside of these zones. Following Parker *et al*. (2007), murre sites within 30 cm of a mirror or rock wall were considered inside those zones. Rock walls were defined as vertical features greater than or equal to the height of a murre in incubation posture. To estimate slope at each egg-laying or territorial site, point elevations taken in the field were used to create 0.15 m contour intervals as well as a Digital Elevation Model (DEM). From this DEM raster surface, a slope surface was created. Each mapped point was then overlayed on the slope surface to acquire the degree of slope for each point. Slopes > 50° were not included in our analyses because murres did not breed there.

Conditions on the rock varied among years. Over time, the murre colony increased in number despite decoys and mirrors being gradually removed. Cormorants nested across the length of the rock during most years except 2003, when only seven cormorant pairs nested on the western end, and 2005 when no cormorants nested. Brown Pelicans roosted within the murre colony on the eastern end of the rock in 2003 and 2005, but not in other years. Our analyses included interaction effects between year and all other variables.

For each of the murre reproductive success parameters, we used logistic regressions to model the outcomes of individual breeding sites in relation to multiple predictors including murre density, average distance to nearest murre egg sites, average distance to nearest cormorant nests, average distance to nearest decoys, presence of rock wall, presence of mirrors, presence of pelicans, degree of slope, egg lay date, and year. Although we hypothesized that any of these covariates could influence reproductive success, we did not have prior knowledge of which combinations of variables would best predict success. We compared multiple logistic regressions based on all combinations of additive effects from these variables and identified potentially useful predictors based on low AICc and high Akaike weights. Models with low AICc values represent a balance between information and model parsimony, i.e., avoiding overfitted models and redundant predictors. Thus, while some of our covariates are correlated, this method selects against models with correlated predictors. We retained covariates that met two criteria: (1) occurred in a model that had lower AICc by a difference exceeding two, compared to the null model without the covariate (ΔAICc > 2); and (2) the importance weight (sum of Akaike weights among models with the covariate) exceeded the proportion of models having that covariate, i.e., 0.5.

Next, we fit additional models based on all combinations of the remaining covariates and their interaction effects with year, again using AICc and weights to retain interaction effects and update the model. We used R statistical software for all AICc-based model

comparisons (R Core Team 2020). Finally, we re-evaluated the selected model with a spatial autocorrelation effects structure; because these models lack a true likelihood calculation preventing further AICc-based comparisons, we used backward stepwise removal until only significant predictors remained at the $\alpha = 0.05$ level (Crawley 2007; PROC GLIMMIX, SAS Institute 2007). Lastly, we corroborated these results using a second model selection approach based on regression trees, which partition continuous predictors into range categories separated by significantly different success rates (Hothorn *et al*. 2006), followed by a refitting with spatial autocorrelation effects.

Initially we included the decoy variable in all years of analysis. However, regressions unexpectedly indicated that shorter distances from decoys were significantly correlated with lower hatching ($\rho = 0.40$) and breeding success ($\rho = 0.25$) in 2005. This year was the only year when decoys were restricted exclusively to the eastern side of the rock where, coincidentally, a large number of roosting Brown Pelicans disrupted breeding murres and caused several birds to abandon breeding sites. Distances to the nearest decoy were lower inside the pelican disturbance (0.24 to 4.3 m) zone compared to outside the disturbance zone (12 to 33 m). Conversely, similar regressions for the other years (2000–2004) had a strong pelican effect and no decoy effect. The relationship with decoys in 2005 was probably obscured by a pelican effect; consequently, we omitted the decoy variable for the remainder of the analysis of 2000–2005 data.

We took a liberal approach in our analysis when addressing independence in reproductive outcomes of repeated breeding sites among years because studies have shown that individual murres generally breed in the same location year after year (Wanless & Harris 1988, Sydeman & Eddy 1995). One potential method of addressing this would have been to include a random effect for breeding site, with the assumption that the same pair was returning to each site. However, this would have reduced our ability to account for spatial autocorrelation effects, which we felt were more important to include in the analysis. The main concern arising from individuals returning to specific breeding sites would be pseudoreplication effects, which could inflate the statistical significance of our results; however, we do not anticipate that this introduced biases in the effect sizes.

RESULTS

During the study period, the DSR murre colony grew from 100 breeding sites in 2000 to a peak of 190 in 2004 (Table 1; since 2004, the colony has grown to about 1 450 breeding pairs). Murres bred mainly in two groups that were highly clustered: one on the eastern half of the rock where the rock was initially recolonized in 1996, and another on the western half (Fig. 1). The eastern group included one dense cluster located between two decoy plots along with several other breeding and territorial sites scattered among decoys. The western group mainly featured a row of breeding sites along the base of an upper wall with several more, including territorial sites, scattered in short rows on the relatively flat surface below them. In most years, Brandt's Cormorant nests were distributed uniformly throughout available habitat both within and beyond the boundaries of the murre breeding areas. Only 28% of murre egg-laying sites occurred adjacent to rock walls. Although five of six of the first murre breeding pairs to re-colonize the rock in 1996 bred within mirror zones (Parker *et al*. 2007), only 8% (range = 0%–25% per year) bred near mirrors in 2000–2005. Although slope varied, most murres chose sites to lay eggs on low- to moderate-grade slopes across the top of the rock (Table 2).

Clustering of egg-laying dates

Global Moran's I statistics indicated spatial autocorrelation of murre egg-laying sites in every year at nearly all distance bands ($Z > 1.96$, $P < 0.05$). Getis-Ord hot spot analyses showed significant spatial clustering of eggs having similar lay dates each year, but only within the denser cluster in the eastern portion of the colony; these sites also tended to be from earlier breeders. We did not detect egg-lay date patterns in other areas of the colony.

Nearest neighbor distances

Average distances to the nearest five to 20 murre breeding sites (Table 2) were highly correlated (correlation coefficient $\rho > 0.84$), as were distances to the nearest one to five cormorant nests ($\rho > 0.49$). Model comparisons revealed that the average distance to the five nearest murre neighbors were more predictive of hatching and breeding success than distances to larger numbers of nearby murre neighbors (ΔAIC > 2.5 and 8.0, respectively). However, the

TABLE 1
Numbers of Common Murre *Uria aalge* breeding and territorial sites, Brandt's Cormorant (BRAC) *Urile penicillatus* nests, decoys, and mirrors, as well as hatching success, fledging success, and breeding success of Common Murres on Devil's Slide Rock, California, USA, 2000–2005

Year	Common Murre		BRAC nests	Decoys	Mirrors	HS[a]	FS[b]	BS[c]
	Breeding sites	Territorial sites						
2000	100	20	81	228	11	0.77	0.94	0.74
2001	113	45	85	186	11	0.78	0.92	0.75
2002	123	43	76	165	8	0.80	0.93	0.77
2003	110	88	7	120	2	0.54	0.95	0.64
2004	190	51	92	106	1	0.72	0.94	0.70
2005	161	84	0	55	1	0.37	0.67	0.32

[a] HS = hatching success (no. of eggs hatched/no. of eggs laid, first clutches only)
[b] FS = fledging success (no. of chicks fledged/no. of chicks hatched)
[c] BS = breeding success (no. of chicks fledged/no. of breeding pairs)

TABLE 2
Description and code names of covariates used to model breeding success of Common Murres *Uria aalge*
from 2000 through 2005, including means, standard deviations (SD), minimum (Min) and maximum (Max) values[a]

Code	Covariate description	Mean	SD	Min	Max
Avg1comu	Distance to nearest murre breeding site	0.21	0.15	0.06	2.40
Avg5comu	Average distance to nearest five murre breeding sites	0.39	0.24	0.14	2.59
Avg20comu	Average distance to nearest 20 murre breeding sites	0.87	0.46	0.27	3.30
kdensity	Murre density (breeding and territorial sites per m^2)	15.75	7.94	4.53	46.02
Avg1brco	Distance to nearest cormorant nest	5.12	7.23	0.05	18.29
Avg5brco	Average distance to nearest five cormorant nests	5.41	7.10	0.49	18.29
Avg1decoy	Average distance to nearest decoy	1.04	2.09	0.02	10.03
Avg10decoy	Average distance to nearest 10 decoys	1.39	2.06	0.22	10.26
DegOfSlope	Degree of slope	17.92	7.73	1.91	48.25
Mirror	Indicator of mirror zone (1 = yes, 0 = no)	0.08	0.28	0	1
Rockwall	Indicator of rock wall zone (1 = yes, 0 = no)	0.28	0.45	0	1
BRPEdisturb	Indicator of pelican disturbance zone (1 = yes, 0 = no)	0.16	0.37	0	1
ELD	Egg lay date (day of year)	28 May	17 d	26 Apr	19 Jul

[a]   *n* = 797 Common Murre nests from 2000 through 2005 (except *n* = 781 nests for egg lay date); distances are in meters.

average distance to the 20 nearest neighbors was more predictive of fledging success than the average distance to five neighbors (ΔAIC = 3.6); therefore, we developed our models based on distances to five and 20 nearest murre neighbors. All distances to cormorant nests (nearest one to 20 neighbors) performed nearly equally well, with similar AIC values (ΔAIC < 2), and we arbitrarily chose the five nearest cormorant nests to represent cormorant distances.

Hatching success

Hatching success was spatially autocorrelated for all first-clutch eggs in all years except 2005, at distances ranging up to ~3.3 m (Global Moran's I). Clustering of high success occurred within the denser cluster of sites in the eastern portion of the colony, while a few clusters of low success occurred in certain outlying portions. Our best logistic regression model, after accounting for spatial correlation, indicated significantly higher hatching success at sites with shorter distances to the nearest five murre sites and at sites that were absent of pelican disturbance (Fig. 2, Table 3). The effect of neighboring murre distances varied by year and was significant in 2001, 2003, and 2004. There was no main effect of egg lay date, although the egg lay date effect varied among years, with higher hatching success for earlier lay dates in 2004 as opposed to later lay dates in 2003. The regression tree analysis identified these same predictors and also indicated that breeding success was positively associated with higher murre site density and shorter distance to cormorant nests.

Fledging success

No spatial autocorrelation was detected in fledging success using Global Moran's I. In both the logistic regression and regression tree analyses, fledging success was best predicted by average distances to the 20 nearest murre sites and the five nearest cormorant nests, with higher success rates occurring at shorter distances from neighboring murre breeding sites (Table 3, Fig. 3).

Breeding success

Spatial autocorrelation in breeding success varied widely among years. In every year, sites that successfully fledged a chick were spatially autocorrelated relative to all murre site locations at maximum distances ranging from 0.3 m (2005) to 3.9 m (2001) (Global Moran's I). In most years, a cluster of successful sites tended to occur within the denser area on the eastern part of the colony, while clusters of unsuccessful sites were concentrated at more outlying parts of the colony. However, clustering was very different in 2005 when the eastern part was highly impacted by pelican disturbance. In that year, clustering of successful sites occurred within the center of the western part of the colony, while much of the eastern part of the colony was in a cluster of failed sites.

Logistic regression, with spatial correlation, indicated significant differences across years, with all years experiencing ≥ 60% breeding success, except for 2005 which experienced a lower degree of success (32%; Table 1). Other predictors varied by year, including significantly higher breeding success related to earlier egg lay dates in 2001, 2002, and 2004, and shorter distances to the nearest five murre breeding sites in 2001, 2003, and 2004 (Table 3; Fig. 3). Breeding site locations within the pelican disturbance zones were also found to have lower breeding success. Consistent with these results, the regression tree also indicated differences among years and higher breeding success associated with earlier egg lay date, shorter distances to five and 20 nearest murre sites, and absence of pelican disturbance. Higher breeding success was also correlated with shorter distance to cormorant nests and higher murre density, but there was no indication that association with mirrors was important.

DISCUSSION

We analyzed the reproductive outcomes of all 100 to 190 active Common Murre breeding sites during 2000 to 2005, for a total of 797 breeding records, at a colony restoration site: Devil's
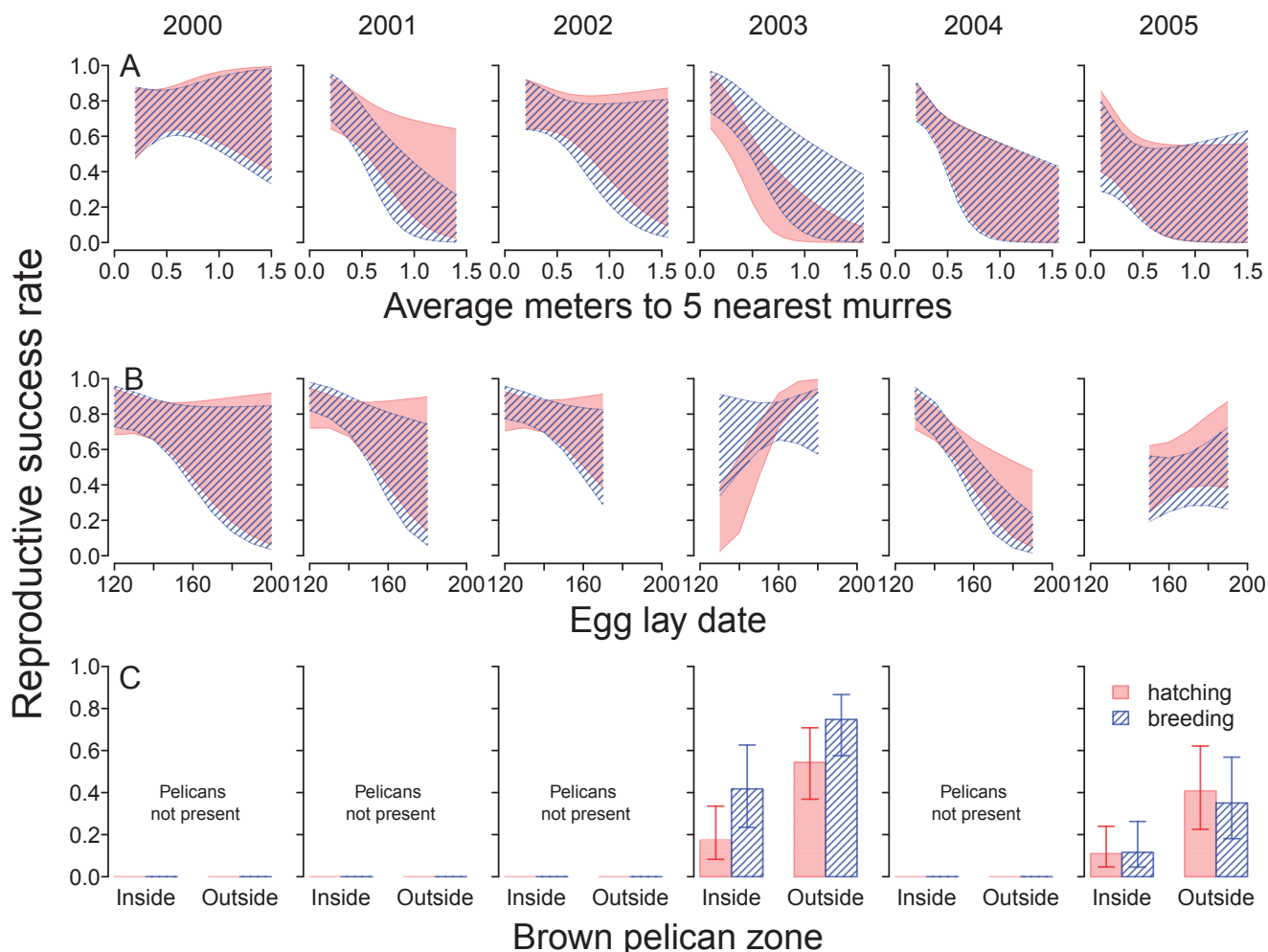
Fig. 2. Hatching success and breeding success of Common Murres *Uria aalge* predicted as a function of: (A) average distance (m) to the five nearest murre breeding sites for each year (significant in 2001, 2003, and 2004 for both parameters; hatching success in solid fill, breeding success in cross fill); (B) egg lay date for each year (significant in 2003 and 2004 for hatching success and 2001, 2003, and 2004 for breeding success); and (C) inside and outside of the Brown Pelican *Pelecanus occidentalis* zone. Predictions are shown as 95% confidence interval bands and were standardized by setting other significant covariates in the predictive models at their mean values (egg lay date 148 [28 May] or 0.39 m average distance to the five nearest murre breeding sites) and modal category (outside of pelican disturbance zone).

Slide Rock. We examined spatial covariates of each breeding site, including physical structure (degree of slope, rock wall), artificial attractants (mirror, decoys), social configurations (distance to neighbors, density of murres), distance to nests of another breeding species (Brandt's Cormorants), and breeding inside or outside areas disturbed by roosting Brown Pelicans. Murre breeding clusters shared similar spatial attributes, confounded with the spatially correlated outcomes detected in analysis using Global Moran's I and Getis Ord cluster tests. We first identified explanatory predictors using a liberal approach that ignored spatial autocorrelations, wherein the outcome of a breeding site was related to the outcomes of proximate neighbors beyond just the effects of site locations. We then eliminated predictors that were not significant when accounting for spatial autocorrelation. Several factors affected murre reproductive success at DSR. In particular, greater reproductive success occurred at sites with earlier egg-laying (except in 2003 and 2005), shorter distances to nearest murre breeding neighbors, shorter distances to nearest cormorant nest neighbors, and at sites not exposed to pelican disturbances. Year was also important for overall breeding success.

With GIS techniques, as well as the small colony expanse, we were able to test for effects that were beyond the immediate vicinity of each laying site, showing that reproductive success can be influenced by factors beyond the immediate breeding site. Murres often breed in large, very dense colonies numbering in the thousands to hundreds of thousands of breeding pairs (Ainley *et al*. 2021). While whole colonies can be exposed to many of the same external factors affecting reproductive success, such as prey availability (Ainley *et al*. 1990, Suryan *et al*. 2006, Chivers *et al*. 2012), breeders can be more prone to factors (such as predators) impacting their reproductive success depending on their location within the colony and the type of breeding site chosen (Parrish 1995, Parrish & Paine 1996). These top-down effects can have major implications for the success of restoration projects or new, naturally-established colonies.

We acknowledge the liberal approach taken with regard to the independence of breeding sites among years, as studies of color-marked birds have shown that individual murres generally lay eggs in the same location annually and even exhibit a tendency towards early or late laying relative to the average (Wanless & Harris 1988,

TABLE 3
Percent change in odds of hatching, fledging, and breeding success estimated
in relationship to significant predictors based on logistic regression[a,b]

Predictors	Estimate	SE	95% CI	t	DF	P
Hatching success						
One nest width (0.15 m) increase in Dist5COMU, by year:						
2000	18%	23%	(-19%, 73%)	0.87	423	0.39
2001	-33%	12%	(-52%, -6%)	-2.29	432	0.02
2002	-17%	12%	(-38%, 11%)	-1.26	576	0.21
2003	-56%	11%	(-76%, -29%)	-3.36	519	< 0.01
2004	-47%	13%	(-67%, -15%)	-2.63	428	0.01
2005	-42%	17%	(-67%, 2%)	-1.91	402	0.06
One week delay in egg lay date, by year:						
2000	-15%	12%	(-36%, 12%)	-1.17	762	0.24
2001	-18%	13%	(-40%, 11%)	-1.30	669	0.19
2002	-10%	12%	(-31%, 17%)	-0.79	750	0.43
2003	142%	54%	57%, 273%	3.99	762	< 0.01
2004	-32%	8%	(-46%, -13%)	-3.14	715	< 0.01
2005	20%	16%	(-8%, 57%)	1.35	715	0.18
Brown Pelican zone	-82%	7%	(-92%, -63%)	-4.58	192	< 0.01
Fledging success						
One nest width (0.15 m) increase in Dist20COMU	-14%	5%	(-22%, -4%)	-2.66	180	0.01
1 m increase in Dist5BRCO	-12%	2%	(-16%, -9%)	-5.99	134	< 0.01
Breeding success						
One nest width (0.15 m) increase in Dist5COMU, by year:						
2000	8%	19%	(-23%, 52%)	0.47	410	0.64
2001	-50%	11%	(-67%, -24%)	-3.29	358	< 0.01
2002	-25%	13%	(-46%, 6%)	-1.64	404	0.10
2003	-44%	11%	(-62%, -18%)	-3.00	343	< 0.01
2004	-49%	14%	(-70%, -14%)	-2.51	368	0.01
2005	-36%	18%	(-62%, 10%)	-1.62	406	0.11
One week delay in egg lay date, by year:						
2000	-22%	11%	(-41%, 3%)	-1.77	761	0.08
2001	-34%	11%	(-52%, -10%)	-2.60	603	0.01
2002	-23%	10%	(-40%, -1%)	-2.06	725	0.04
2003	11%	19%	(-21%, 55%)	0.58	761	0.56
2004	-43%	7%	(-56%, -27%)	-4.41	743	< 0.01
2005	10%	13%	(-13%, 40%)	0.82	750	0.41
Mirror zone	-59%	15%	(-80%, -15%)	-2.38	528	0.02
Brown Pelican zone	-76%	9%	(-89%, -49%)	-3.73	163	< 0.01

[a]　Standard errors (SE), confidence intervals (CI), *t*-statistics (*t*), degrees of freedom (DF), and *P* values (*P*) were adjusted for spatially autocorrelated data.

[b]　See Table 2 for covariate codes.

Sydeman & Eddy 1995). Murre breeding success tends to be higher at sites used for many years, partly because of the experience of site holders (i.e., individual quality; Harris *et al*. 1997) and also because of greater habitat (or site) quality (Kokko *et al*. 2004). The effects of highly productive or less productive individuals using the same breeding sites repeatedly, exacerbated by the small size of our study

colony, may have contributed to the consistency of these patterns throughout the sample of sites that we analyzed, thereby inflating the statistical strength in our findings. By including egg lay date as a predictor, our models account for some of these individual differences, but we were unable to measure the overall extent of individual autocorrelations because birds were not marked. Our
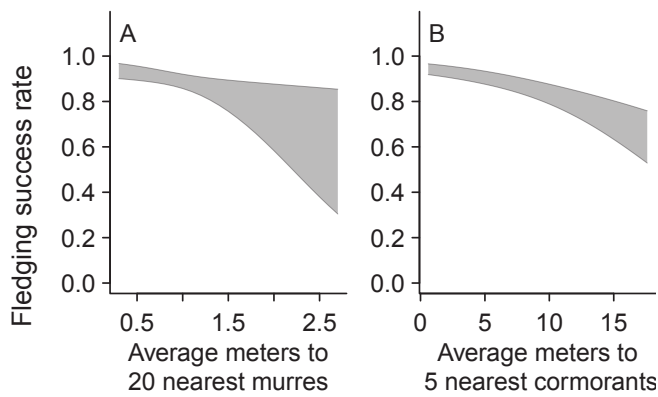
Fig. 3. Fledging success of Common Murres *Uria aalge* predicted as a function of (A) average distance to the 20 nearest murre nests, standardized based on mean average distance to the five nearest cormorant nests (5.4 m); and (B) average distance to the five nearest cormorant nests, standardized by setting significant average distance to the 20 nearest murre nests at its mean value 0.87 m. Predictions are shown with 95% confidence interval band.

analysis assumes that individual differences derived by timing and site location are largely accounted for by the effects of directly measurable factors such as egg lay date and spatial covariates. Lacking marked individuals, our results should be considered in the context of this assumption.

We found that local breeding density was the most consistent predictor of murre reproductive success. Murres breeding in dense clusters (lower nearest neighbor distances) had greater breeding success compared to those occupying the perimeter of the colony (higher nearest neighbor distances). Previous studies reported that higher densities of breeding murres were associated with a positive effect on reproductive success (Birkhead 1977, Gaston & Nettleship 1981, Birkhead *et al*. 1985, Hatchwell 1991, Gaston & Elliott 1996, Harris *et al*. 1997). Murres typically breed in tight clusters to defend breeding sites from predators (e.g., eagles, gulls, and corvids; Birkhead 1977, Hatchwell 1991; Parrish 1995) and space competitors (e.g., Brandt's Cormorants; Boekelheide *et al*. 1990a, 1990b); in concert, behavioral adaptations allow relatively large numbers of murres to occupy suitable breeding habitats. These behaviors may also facilitate low breeding site disturbance/predation and more long-term colony persistence. In addition, dense clustering and high breeding success may have encouraged prospecting birds to join the colony, fostering faster colony growth, as has been observed in other seabird species (Danchin *et al*. 1998, Valone & Templeton 2002).

Similar and earlier egg-laying dates were clustered in the densest portion of the colony. Laying dates where the colony was most dense tended to be earlier than average for the colony (USFWS, unpubl. data). This dense cluster occurred at the location where at least 127 remaining birds were documented in 1987 (following extirpation from breeding in 1986) and where the first breeding sites were re-established in 1996–1998. Thus, this cluster likely included older individuals with past experience at the colony (Carter *et al*. 2001, 2003a; Parker *et al*. 2007). For the colony, reproductive success generally declined with later egg laying, with the exceptions of hatching and breeding success in 2003 and 2005 (Fig. 2). In 2003 and 2005, low springtime upwelling of cold water resulted in reduced prey availability (Goericke *et al*. 2004, Peterson

et al. 2006), leading to delayed breeding, with several early breeders abandoning their eggs shortly after laying.

Other studies of Common Murres have also shown that early to mid-season breeders tend to have higher reproductive success than later breeders, which is partly associated with prey availability for chick-rearing but is also related to adult age and experience, individual quality, breeding site location within the colony, and possibly other factors (Wanless & Harris 1988, Boekelheide *et al*. 1990b, Hatchwell 1991, Shultz *et al*. 2009, Ainley *et al*. 2021). Breeding synchrony within a colony is likely beneficial; earliest and latest breeders, or those out of synchrony with immediate neighbors, are easier targets for predators (Birkhead 1977, Hatchwell 1991, Murphy & Schauer 1996) or are subject to unfavorable environmental conditions early or late in the breeding season (e.g., Gaston and Nettleship 1981). Within the recently re-established colony at DSR, timing of breeding may be influenced by breeding age and experience of murres within dense clusters, with many first-time breeders outside of these clusters. Earlier breeding often reflects older and more experienced birds, which tend to have higher reproductive success (Boekelheide *et al*. 1990b, Ainley *et al*. 2021). At DSR, many sites first established outside dense clusters were not used in subsequent years, whereas breeding sites within clusters tended to occur in the same locations across years. This situation was also affected by our annual modifications in decoy placement to encourage development of dense breeding clusters.

The positive effect of breeding near Brandt's Cormorants was not entirely surprising. Brandt's Cormorants often nest in mixed colonies with murres in the California Current System. In California, nesting cormorants often precede murre colonization or re-colonization events (McChesney *et al*. 1998, 1999; Carter *et al*. 2001; Manuwal & Carter 2001; Capitolo *et al*. 2005; USFWS, unpubl. data). Along with the likelihood of small numbers of survivors from the extirpated colony and adequate local prey availability, rapid re-establishment of breeding murres on DSR in 1996 was likely influenced by the colonization by cormorants that occurred 1993–1995 after space had been created by the loss of the DSR murre colony in 1986 (Carter *et al*. 2003a, Parker *et al*. 2007). Cormorant nests tended to be in or near the same locations, even if not occupied by the same individual, across years and with high breeding success, leading to fairly stable spatial attributes for murres and allowing long-term use of specific murre breeding sites. The cormorants' larger size and greater ability to repel avian predators and other space competitors (e.g., pelicans) likely helped protect murres from disturbance and egg/chick predation when murres were breeding in low numbers (Capitolo *et al*. 2005). In this way, the cormorants could be considered a protective species for murres. Several other studies have shown increased reproductive success in birds as a result of a protective species, usually in the form of reduced predation or disturbance (Quinn & Ueta 2008, Morandini *et al*. 2020). For example, Common Murres breeding near Peregrine Falcons *Falco peregrinus* have benefitted from reduced Bald Eagle *Haliaeetus leucocephalus* disturbance and predation (Hipfner *et al*. 2011).

Pelicans, and more frequently non-breeding cormorants, occasionally roosted on the eastern edge of DSR, out of reach of nesting cormorants' defensive strikes. However, in 2003 and 2005, when nesting cormorants were absent or nearly so, individual pelicans sometimes walked into or landed among breeding murres. Fairly large disruptions resulted in egg or chick loss at several murre sites, while several other occupied sites were abandoned prior to egg laying. Impacts from pelican disturbance were greatest in 2005 when murre breeding density and success were also reduced by poor foraging conditions (Peterson *et al*. 2006). Nine

observed egg losses in 2005 were attributed to pelican disturbance (15% of 62 known failed egg fates in 2000–2005). Pelican disturbance partially explained low hatching and breeding success for murres in 2000–2005 (Table 3; Fig. 2).

California Brown Pelicans *P. o. occidentalis* breed from southern California to Nayarit, Mexico (Shields 2002), but non-breeding and post-breeding birds are common on the central California coast from spring through fall. Pelican disturbance has also been related to massive abandonment at other murre colonies in central California and Oregon in certain years (Thayer *et al*. 1999; Carter *et al*. 2003b; Horton & Suryan 2012; USFWS, unpubl. data). This subspecies has recovered from large declines caused by Dichlorodiphenyldichloroethylene (DDE) poisoning in the 1950s to early 1970s (Shields 2002). Due to larger populations of pelicans in the California Current System, the potential for pelican disturbances to murre colonies has increased. Since the time of this study, pelican disturbance to the DSR and other central California colonies has continued to occur in some years (USFWS, unpubl. data). Similarly, numerous colonies of seabirds have been impacted by long-term disturbance and predation caused by sea eagles, although several populations of seabirds have recovered from past declines (Hipfner *et al*. 2012). For example, frequent disturbance and predation from Bald Eagles have resulted in the total to near abandonment of several Common Murre colonies in the Pacific Northwest. Eagles flush murres from breeding sites, directly prey on murres, and allow easy colony access for predators such as gulls and corvids to scavenge eggs and chicks (Parrish & Paine 1996, Hipfner *et al*. 2012).

While it was initially thought that decoys and mirrors, along with automated playbacks of murre vocalizations, were essential in the DSR restoration project (Parker *et al*. 2007), we found no significant role of these elements in the breeding success of the growing colony in the 2000–2005 period. Apparently, once the colony reached a social facilitation saturation, more artificial stimulus was not necessary.

We found no relationship between reproductive success of murres and slope or proximity to rock walls, in contrast to the findings of others (Gaston & Nettleship 1981, Birkhead *et al*. 1985, Gaston & Elliott 1996, Harris *et al*. 1997). Rock walls can help reduce avian predation and the likelihood of an egg rolling off the breeding site. On DSR, although many decoys were purposefully aligned to encourage early colonists to use rock walls, only 28% of breeding sites in 2000–2005 were immediately adjacent to a rock wall, and most breeding sites abutted only one wall. Initial colonizers (1996–1999) preferred to breed within space provided among the decoys and adjacent to other live murres as opposed to breeding immediately against rock walls (Parker *et al*. 2007, USFWS unpubl. data). The gently-sloped top of DSR likely removed many possible benefits of rock walls, making other factors more important for reproductive success. As most large murre colonies in the California Current System are on flatter to gently sloped habitats (Carter *et al*. 2001), sites with these characteristics appear to offer the best quality habitat.

CONCLUSIONS

The goal of seabird colony restoration projects is to develop self-sustaining populations (Jones & Kress 2012). Because of their breeding habitat requirements, high breeding colony fidelity, and semi-precocial chick rearing, the restoration of murre colonies poses challenges that are not faced by species with low colony fidelity or that permit chick translocations (Jones & Kress 2012). Thus, murre

colony restoration efforts, apart from eliminating the threats that caused initial colony loss, rely primarily on social attraction.

Substantial colony growth at DSR since 1999 partly reflected high breeding success similar to nearby long-established colonies (Ainley *et al*. 1990, Kappes *et al*. 2011), despite the small colony size and the colony comprising many young and inexperienced breeders. For the newly re-established colony of murres at DSR, besides being in close proximity to large murre colonies in the region, we found that several spatial factors were associated with reproductive success, including breeding in close proximity to neighboring murres and Brandt's Cormorants, breeding in portions of the colony with earlier egg-laying dates, and breeding away from areas impacted by disturbance. This finding supports a restoration strategy seeking to form larger and denser "core" breeding groups of murres instead of several more dispersed groups. Future murre restoration projects using social attraction techniques might consider designs that initially focus on the creation of just one or two core breeding groups, preferably in the last area occupied prior to extirpation (if known). In the DSR case, the best available habitat may have been the last portion of the rock attended by murres in 1986–87 as the colony was being extirpated. However, our formation of two core breeding groups on the eastern and western sides of the rock, respectively, proved beneficial in years when pelican disturbance impacted breeding success in one portion of the colony only (i.e., dispersed risk). Use of historical information, such as photos, to identify former core breeding areas should be utilized whenever possible.

Within the California Current System portion of the murre range, selecting locations with frequent nesting by Brandt's Cormorants may benefit any murre restoration project, as cormorants play a role in attracting early recruits and can promote breeding success. Alternatively, enhancing Brandt's Cormorant nesting using similar social attraction techniques (e.g., decoys, decoy nests, vocalizations) may be another method to increase success at attracting murres. Unless mitigation measures can be employed, habitats known to be utilized by roosting Brown Pelicans, other large and potentially aggressive species such as Bald Eagles, large corvids, and sea lions (which have impacted murre colonies in California; Boekelheide *et al*. 1990b, Thibault *et al*. 2010), mammalian predators, and humans are best avoided due to potential impacts from disturbance or predation.

To expand on the points made above, we provide an example of an unsuccessful attempt to restore breeding murres to San Pedro Rock, located only 2 km from DSR. San Pedro Rock held a murre colony until it was extirpated by commercial eggers in the early 20th century (Ray 1909). Between 1998 and 2004, we used very similar social attraction techniques at DSR with the intention of re-establishing breeding murres to San Pedro Rock. Brandt's Cormorant decoys and decoy nests were added amongst the murre decoys in 2003–2004 in hopes of establishing cormorant nesting and increasing success at establishing breeding murres. Unfortunately, murres only occasionally visited San Pedro Rock during the seven seasons of social attraction efforts, and little breeding-related behaviors were observed. Cormorants were never seen visiting the decoy area despite roosting on other parts of the rock. We believe a combination of factors prevented rapid re-colonization of San Pedro Rock by murres, including: (1) lack of recent breeding—no live birds had a history of breeding or hatching on San Pedro Rock; (2) lack of Brandt's Cormorant nesting; and (3) a pair of predatory Common Ravens nesting on the rock. Ravens frequented the decoy area and were attracted to the mirrors to the point that we had to remove the mirrors.

We recognize that the factors influencing murre colonization and reproductive success at DSR may be specific to this location and to neighboring colonies in the Gulf of the Farallones. Colonies and potential restoration sites outside the region may experience very different circumstances; for example, murres may position themselves primarily on cliff ledges or they may nest where Brandt's Cormorants do not occur. Thus, evaluating local conditions before investing in murre restoration work is essential to designing a successful project.

ACKNOWLEDGEMENTS

REFERENCES

AINLEY, D.G. 1990. Farallon seabirds: Patterns at the community level. In: AINLEY, D.G. & R.J. BOEKELHEIDE (Eds.) *Seabirds of the Farallon Islands: Ecology, Dynamics, and Structure of an Upwelling-system Community*. Stanford, USA: Stanford University Press.

AINLEY, D.G., NETTLESHIP, D.N. & STOREY, A.E. (2021). Common Murre (*Uria aalge*), version 2.0. In: BILLERMAN, S.M., RODEWALD, P.G. & KEENEY, B.K. (Eds.) *Birds of the World*. Ithaca, USA: Cornell Lab of Ornithology. doi:10.2173/bow.commur.02

BIRKHEAD, T. R. 1977. The effect of habitat and density on breeding success in the Common Guillemot (*Uria aalge*). *Journal of Animal Ecology* 46: 751–764.

BIRKHEAD, T.R., GREENE, E., BIGGINS, J.D. & NETTLESHIP, D.N. 1985. Breeding site characteristics and breeding success in Thick-billed Murres. *Canadian Journal of Zoology* 63: 1880–1884.

BOEKELHEIDE, R.J, AINLEY, D.G., MORRELL, S.H. & LEWIS, T.J. 1990a. Brandt's Cormorant. In: AINLEY, D.G. & BOEKELHEIDE, R.J. (Eds.) *Seabirds of the Farallon Islands: Ecology, Dynamics, and Structure of an Upwelling-system Community*. Stanford, USA: Stanford University Press.

BOEKELHEIDE, R.J, AINLEY, D.G., MORRELL, S.H., HUBER, H.R. & LEWIS, T.J. 1990b. Common Murre. In: AINLEY, D.G. & BOEKELHEIDE, R.J. (Eds.) *Seabirds of the Farallon Islands: Ecology, Dynamics, and Structure of an Upwelling-system Community*. Stanford, USA: Stanford University Press.

BRIGGS, K.T., TYLER, W.B., LEWIS, D.B. & DETTMAN, K.F. 1983. *Seabirds of central and northern California, 1980–1983: Status, abundance and distribution*. Final Report. Santa Cruz, USA: University of California, Center for Marine Studies.

BURNHAM, K.P. & ANDERSON, D.R. 2002. *Model Selection and Inference: A Practical Information-Theoretic Approach*. Second Edition. New York, USA: Springer-Verlag New York, Inc.

CAPITOLO, P.J., CARTER, H.R., McCHESNEY, G.J. & PARKER, M.W. 2005. Common Murres prospecting within cormorant colonies in Del Norte and Humboldt counties, California, 1996 to 2004. *Northwestern Naturalist* 86: 144–150.

CARTER, H.R., WILSON, U.W., LOWE, R.W. ET AL. 2001. Population trends of the Common Murre (*Uria aalge californica*). In: MANUWAL, D.A., CARTER, H.R., ZIMMERMAN, T.S. & ORTHMEYER, D.L. (Eds.) *Biology and Conservation of the Common Murre in California, Oregon, Washington, and British Columbia*. Volume 1: Natural history and population trends. Washington, D.C.: US Geological Survey, Information and Technology Report USGS/BRD/ITR-2000-0012.

CARTER, H.R., LEE, V.A., PAGE, G.W. ET AL. 2003a. The 1986 *Apex* Houston oil spill in central California: Seabird injury assessment and litigation process. *Marine Ornithology* 31: 9–19.

CARTER, H.R., CAPITOLO, P.J., PARKER, M.W., GOLIGHTLY, R.T. & YEE, J. 2003b. Population impacts to Common Murres at the Drake's Bay colony complex, California. In: CARTER, H.R. & GOLIGHTLY, R.T. (Eds.) *Seabird Injuries from the 1997–1998 Point Reyes Tarball Incident*. Unpublished report. Arcata, USA: Humboldt State University, Department of Wildlife.

CHIVERS, L.S., LUNDY, M.G. & REID, N. 2012. Stable breeding despite variable feeding in two sympatric auk (Alcidae) species. *Bird Study*. 59: 67–73. doi:10.1080/00063657.2011.632618

CRAWLEY, M.J. 2007. *The R Book*. Chichester, England: John Wiley and Sons Limited.

DANCHIN, E., BOULINER, T. & MASSOT, M. 1998. Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. *Ecology* 79: 2415–2428.

GASTON, A.J. & ELLIOTT, R.D. 1996. Predation by ravens *Corvus corax* on Brunnich's Guillemot *Uria lomvia* eggs and chicks and its possible impact on breeding site selection. *Ibis* 138: 742–748.

GASTON, A.J. & NETTLESHIP, D.N. 1981. *The Thick-billed Murres of Prince Leopold Island*. Wildlife Monograph No. 6. Ottawa, Canada: Canadian Wildlife Service.

GOERICKE, R., BOGRAD, S.J., GAXIOLO-CASTRO, G. ET AL. 2004. The state of the California Current 2003–2004: a rare "normal" year. *California Cooperative Fisheries Investigations Reports* 45: 27–60.

HARRIS, M.P., WANLESS, S., BARTON, T.R. & ELSTON, D.A. 1997. Nest site characteristics, duration of use and breeding success in the guillemot *Uria aalge*. *Ibis* 139: 468–476.

HATCHWELL, B.J. 1991. An experimental study of the effects of timing of breeding on the reproductive success of Common Guillemots (*Uria aalge*). *Journal of Animal Ecology* 60: 721–736.

HIPFNER, J.M., MORRISON, K.W. & DARVILL, R. 2011. Peregrine Falcons enable two species of colonial seabirds to breed successfully by excluding other aerial predators. *Waterbirds* 34: 82–88.

HIPFNER, J.M., BLIGHT, L.K., LOWE, R.W. ET AL. 2012. Unintended consequences: how the recovery of sea eagle *Haliaeetus* spp. populations in the northern hemisphere is affecting seabirds. *Marine Ornithology* 40: 39–52.

HORTON, C.A. & SURYAN, R.M. 2012. Brown Pelicans: A new disturbance source to breeding Common Murres in Oregon? *Oregon Birds* 38: 84–88.

HOTHORN, T., HORNIK, K. & ZEILEIS, A. 2006. Unbiased recursive partitioning: a conditional inference framework. *Journal of Computational and Graphical Statistics* 15: 651–674.

JONES, H.P. & KRESS, S.W. 2012. A review of the world's active seabird restoration projects. *Journal of Wildlife Management* 76: 2–9.

KAPPES, P.J., MCCHESNEY, G.J., PARKER, M.W., CARTER, H.R., KRESS, S.W. & GOLIGHTLY, R.T. 2011. Use of time-activity budgets to measure early progress of a social attraction restoration project. *Biological Conservation* 144: 620–626.

KOKKO, H., HARRIS, M.P. & WANLESS, S. 2004. Competition for breeding sites and site-dependent population regulation in a highly colonial seabird, the Common Guillemot *Uria aalge*. *Journal of Animal Ecology* 73: 367–376.

KRESS, S.W. 1998. Applying research for effective management: Case studies in seabird restoration. In: MARZLUFF, J.M. & SALLABANKS, R. (Eds.) *Avian Conservation: Research and Management.* Washington, USA: Island Press.

KRESS, S.W. & NETTLESHIP, D.N. 1988. Re-establishment of Atlantic Puffins (*Fraterula artica*) at a former breeding site in the Gulf of Maine. *Journal of Field Ornithology* 59: 161–170.

MANUWAL, D.A. & CARTER, H.R. 2001. The natural history of the Common Murre (*Uria aalge californica*). In: MANUWAL, D.A., CARTER, H.R., ZIMMERMAN, T.S. & ORTHMEYER, D.L. (Eds.) *Biology and Conservation of the Common Murre in California, Oregon, Washington, and British Columbia. Volume 1: Natural history and population trends.* Washington, USA: US Geological Survey, Information and Technology Report USGS/BRD/ITR-2000-0012.

MCCHESNEY, G.J., CARTER, H R., PARKER, M.W., TAKEKAWA, J.E. &. YEE, J.L. 1998. *Population trends and subcolony use of Common Murres and Brandt's Cormorants at Point Reyes Headlands, California, 1979–1997.* Unpublished report. Dixon, USA: US Geological Survey, Biological Resources Division, Western Ecological Research Center; Arcata, USA: Humboldt State University, Department of Wildlife; Newark, USA: US Fish and Wildlife Service, San Francisco Bay National Wildlife Refuge Complex.

MCCHESNEY, G.J, CARTER, H.R., PARKER M.W., CAPITOLO, P.J., TAKEKAWA, J.E. & YEE, J.L. 1999. *Population trends and subcolony use of Common Murres and Brandt's Cormorants at the Castle/Hurricane Colony Complex, California 1979–1997.* Unpublished report. Dixon, USA: US Geological Survey, Biological Resources Division, Western Ecological Research Center; Arcata, USA: Humboldt State University, Department of Wildlife; Newark, USA: US Fish and Wildlife Service, San Francisco Bay National Wildlife Refuge Complex.

MORANDINI, V., DUGGER, K.M., AINLEY, D. & FERRER, M. 2020. Rockhopper Penguin–Imperial Cormorant mixed colonies in the Falkland Islands: a stroke of luck for late breeders. *Ecosphere* 11: e03272. doi:10.1002/ecs2.3272

MURPHY, E.C. & SCHAUER, J.H. 1996. Synchrony in egg-laying and reproductive success of neighboring Common Murres, *Uria aalge*. *Behavioral Ecology and Sociobiology* 39: 245–258.

PARKER, M.W., KRESS, S.W., GOLIGHTLY, R.T. ET AL. 2007. Assessment of social attraction techniques used to restore a Common Murre colony in central California. *Waterbirds* 30: 17–28.

PARRISH, J.K. 1995. Influence of group size and habitat type on reproductive success in Common Murres (*Uria aalge*). *The Auk* 112: 390–401.

PARRISH, J. & PAINE, R.T. 1996. Ecological interactions and habitat modification in nesting Common Murres. *Bird Conservation International* 6: 261–269.

PETERSON, W.T., EMMETT, R., GOERICKE R. ET AL. 2006. The state of the California Current, 2005–2006: warm in the north, cool in the south. *California Cooperative Fisheries Investigations Reports* 47: 30–74.

QUINN, J.L. & UETA, M. 2008. Protective nesting associations in birds. *Ibis 150 (Suppl. 1)*: 146–167.

R CORE TEAM. 2020. *R: A language and environment for statistical computing.* Vienna, Austria: The R Foundation for Statistical Computing. [Available online at: https://www.R-project.org/. Accessed on 01 July 2020.]

RAY, M.S. 1909. The passing of the Pedro Island sea-bird rookery. *The Condor* 11: 94–96.

SAS INSTITUTE. 2007. *SAS OnlineDoc® 9.2.* Cary, USA: SAS Institute Inc.

SHULTZ, M.T., PIATT, J.F., HARDING, A.M.A., KETTLE, A.B. & VAN PELT, T.I. 2009. Timing of breeding and reproductive performance in murres and kittiwakes reflect mismatched seasonal prey dynamics. *Marine Ecology Progress Series* 393: 247–258. doi:10.3354/meps08136

SHIELDS, M. 2002. Brown Pelican (*Pelecanus occidentalis*). In: POOLE, A. & F. GILL (Eds.) *The Birds of North America, No. 609.* Philadelphia, USA: The Birds of North America, Inc.

SOWLS, A.L., DEGANGE, A.R., NELSON, J.W. & LESTER, G.S. 1980. *Catalog of California Seabird Colonies.* FWS/OBS 37/80. Washington, USA: US Fish and Wildlife Service, Biological Services Program.

SURYAN, R.M., IRONS, D.B., BROWN, E.D., JODICE, P.G.R. & ROBY, D.D. 2006. Site-specific effects on productivity of an upper trophic-level marine predator: Bottom-up, top-down, and mismatch effects on reproduction in a colonial seabird. *Progress in Oceanography* 68: 303–328.

SYDEMAN, W.J. & J.O. EDDY. 1995. Repeatability in laying date and its relationship to individual quality for Common Murres. *The Condor* 97: 1048–1052.

TAKEKAWA, J.E., CARTER, H.R. & HARVEY, T.E. 1990. Decline of the Common Murre in central California 1980–1986. *Studies in Avian Biology* 14: 149–163.

THAYER, J.A., SYDEMAN, W.J., FAIRMAN, N.P. & ALLEN, S.G. 1999. Attendance and effects of disturbance on coastal Common Murre colonies at Point Reyes, California. *Waterbirds* 22: 130–139.

THIBAULT, J.M., MCCHESNEY, G.J., GOLIGHTLY, R.T., GOLEY, P.D. & CARTER, H.R. 2010. *Decline of the Common Murre colony at Redding Rock, California, and restoration options.* Unpublished report. Newark, USA: US Fish and Wildlife Service, San Francisco Bay National Wildlife Refuge Complex; Arcata, USA: Humboldt State University, Departments of Wildlife and Biological Sciences.

VALONE, T.J. & TEMPLETON, J.J. 2002. Public information for the assessment of quality: a widespread social phenomenon. *Philosophical Transactions for the Royal Society of London B* 357: 1549–1557.

WANLESS, S. & HARRIS, M.P. 1988. The importance of relative laying date on breeding success of the guillemot *Uria aalge*. *Ornis Scandinavica* 19: 205–211.