An Analysis of the Probability of Recolonization of Picher Canyon by Great Egrets: Effects of Temporal Scale and Human Activity

John P. Kelly[1]
Cypress Grove Research Center, Audubon Canyon Ranch
[1]Email: kellyjp@egret.org

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Cypress Grove Research Center
P. O. Box 808, Marshall, CA 94940

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SUMMARY

Fifty-four Great Egret colonies were active in the northern San Francisco Bay area for one or more years, 1991-2011, with an average of 21±0.8 (SE) active colonies each year. The occupation of sites that were recolonized after abandonment represented 5.0 ±1.1% of regional site use, over all sites and years, and included sites that were abandoned for up to 13 years. Logistic regression suggested increases in the probability of recolonization with increases in the historic size of the nesting colony, the presence of other nesting heron or egret species, and the number of Great Egret nests immediately prior to abandonment. In addition, the odds of recolonization were predicted to decline by 10% annually with each successive year of abandonment and by over half with each unit increase among four levels of human activity. The results predicted recolonization of Picher Canyon within ten years, if human activity is managed as a remote, rural site, and a recolonization probability exceeding 50% over time spans greater than ten years if human activity is consistent with "low-density rural residential" conditions in the region. Although these predictions are subject to considerable uncertainty, they highlight the potentially important effects of management on the recolonization of abandoned heronries. The management implications of these results are consistent with the recommendations of the Picher Canyon Management Framework (Millus et al. 2013).

INTRODUCTION

A dramatic decline in Great Egret (*Ardea alba*) nesting activity occurred during the 2013 season in the Picher Canyon heronry at the Martin Griffin Preserve of Audubon Canyon Ranch, Stinson Beach, CA. The decline was characterized by a marked reduction in the number of initiated nests, from 75 nests in 2012 to 32 nests in 2013, and a complete failure of all nest attempts (Millus et al. 2013). Similar catastrophic declines in nest abundance at other colony sites in the San Francisco Bay area have resulted in complete abandonment of the sites in subsequent years (Kelly et al. 2007). Total reproductive failure is unprecedented at Picher Canyon and has led to serious concerns about the future viability of ACR's Martin Griffin Preserve as a nesting colony site for Great Egrets.

From a preserve stewardship perspective, concerns about the viability of the Picher Canyon heronry are focused on the extent to which the Canyon continues to provide suitable habitat for nesting herons and egrets. Two key questions are:

- What is the appropriate scope of management and use of Picher Canyon needed to sustain, restore, or enhance habitat values for nesting herons and egrets?
- What is the likelihood that appropriate management will lead to recolonization if the site is abandoned in 2014?

This report augments and updates preliminary estimates of regional recolonization rates presented to the ACR Board of Directors in April 2014. I address the two questions above, based on general patterns of colony site abandonment, recolonization, and observed levels of human activity in the northern San Francisco Bay area, 1991-2011 (more recent field observations have been gathered but are unavailable because of a data-processing lag).

The most likely primary cause of the 2013 nesting failure was disturbance by potential avian nest predators, particularly disturbance by Bald Eagle (*Haliaeetus leucocephalus*; Millus et al. 2013). Disturbance of the heronry by other avian nest predators has been observed frequently since 1967 (Pratt and Winkler 1985, Kelly et al, 2005, 2007; Rothenbach and Kelly 2012). No substantial changes in habitat quality for nesting herons and egrets have been observed, although future conditions could include additional disturbance by potential nest predators or humans. Therefore, given the historic value of Picher Canyon to nesting herons and egrets, their consistent use of other traditional colony sites in areas that differ in the extent of nearby human activity, and their occasional recolonization of abandoned sites, the potential effects of preserve management on the probability of recolonization is an important consideration in responsible stewardship. In addition, because protection of the heronry in Picher Canyon was the original cause that led to the establishment of Audubon Canyon Ranch, the strength of ACR's longstanding vision to promote the protection of natural areas may be tested by the appropriateness of its management response to the colony decline.

Nesting herons and egrets are strongly colonial and exhibit patterns of site selection that are marked by the continuing use of traditional colony sites. Such choices reflect not only the selection of preferred habitat conditions and nesting locations (Kelly et al. 2008), but also numerous potential benefits directly related to the presence of other nesting individuals (e.g., predator protection, foraging enhancement, access to mates, etc.; Wittenberger and Hunt 1985). Although individual egrets may return to colony sites used in the previous year, they also exhibit a readiness to relocate adaptively between years. This leads to substantial annual variation in the sizes of nesting colonies. In choosing among prospective colony sites, they are likely to be highly selective and sensitive to changing conditions.

The recolonization of abandoned sites depends on colony-site choices made by first-time breeders and by adult birds that do not to return to the colony sites they used in the previous year. In contrast to the choices Great Egrets make in selecting among active colony sites, individuals that choose to nest in abandoned sites must base their colony-site preferences on criteria unrelated to the presence of other nesting individuals. The extent to which recolonization might be influenced by the return of individuals that previously abandoned the site to nest elsewhere is unknown.

A few heron and egret colony sites in the San Francisco Bay area are abandoned or recolonized in most years, but such occurrences are relatively infrequent compared to the generally consistent annual use of active colony sites (Kelly et al. 2007). Therefore, the available information on recolonization rates in the region is limited and, given the difficulty of estimating the probability of infrequent events, I strongly emphasize a cautious approach when interpreting the results in this report. In addition, changes in regional population growth, habitat conditions at other colony sites, productivity among wetland feeding areas, regional patterns of human disturbance, predation pressure, and other processes affecting the feeding or nesting behaviors of herons and egrets, may dramatically increase or decrease the likelihood of recolonization in any year and are not included in this analysis. The potential effects of such processes underscore the need for cautious interpretation of the probabilities estimated in this report. In spite of considerable uncertainty, the estimated probabilities provide the best available basis for stewardship planning at ACR's Martin Griffin Preserve.

METHODS

Regional reuse, abandonment, and recolonization of colony sites

I calculated the overall regional probabilities that active Great Egret colonies would be established at recolonized sites (abandoned for at least one nesting season, then reoccupied), at newly colonized sites, and at sites that were active in the previous season, 1991-2011 (n = 418). These probabilities (reported as percents), were simply pooled across all colony sites and years of study, with standard errors (SE) reflecting random variation among sites and years, ignoring possible differences among subregions, annual trends, or the effects weather, food availability, disturbance, or other factors that might influence colony site selection by herons and egrets.

Recolonization Probability

The suitability of each colony site may depend on numerous, unique aspects of its nesting history, habitat quality, geographic location, surrounding foraging landscape, and other ecological conditions. However, the specific chance of recolonization in Picher Canyon cannot be determined from ACR's intensive studies of nesting activity in the Canyon since 1967. The chance of recolonization, at any particular colony site, must be measured in relation to repeated outcomes across many other sites.

I used logistic regression to model the effects of key predictors of recolonization, using outcomes of recolonization vs. no recolonization as the response variable. Recolonization probabilities were modeled in relation to the number of colony-site-years that followed colony-site abandonments by Great Egrets, in the northern San Francisco Bay area, 1991-2011 (n = 280 colony-site-years, excluding occupied colony-site-years). The data were weighted by the annual number of abandoned sites that were followed. The resulting model can be used to predict the probability of recolonization given the set of conditions at a particular site, such as at Picher Canyon.

Candidate predictors of recolonization by Great Egrets included: (1) number of consecutive years Great Egrets nested at the site prior to abandonment; (2) presence or absence of other nesting heron or egret species (Ardeidae); (3) maximum known Great Egret colony size; (4) mean Great Egret colony size across five nesting seasons immediately prior to abandonment; (5) total number of years (before abandonment) that Great Egrets are known to have nested at the colony site; and (6) number of Great Egret nests immediately prior to abandonment. In addition, I decided, *a priori*, to include two additional predictors in the model, because of their particular relevance to the future management of the Martin Griffin Preserve: (1) number of years after abandonment, to address the probability of future recolonization over increasing year-spans and (2) level of human activity within approximately 300 m, suggested by documented effects of human activity on colony site selection by Ardeids (e.g., Gibbs et al. 1987, Watts and Bradshaw 1994).

To account for differences in human activity, I classified each colony site according to the most appropriate of the following ordinal categories: 1 = remote, agricultural, or very low-density rural; 2 = low-density rural residential; 3 = medium-density residential neighborhoods; 4 = intensively used public parks, schools, or high-density residential or commercial development. Colony sites classified as Level 4 included Alcatraz Island, Napa State Hospital, and West 9th Street in Santa Rosa. The estimated model parameters were not biased by conditions at Picher Canyon because Picher Canyon was not used in the analysis (Great Egrets are not known to have previously abandoned this site).

To identify the best-performing set of predictors, given the data, I ran preliminary models using all possible subsets of the candidate variables, including the two *a priori* variables for human activity and consecutive years of abandonment, in each model, and selected the best-performing model based on comparisons of associated AIC values (Burnham and Anderson 2002). All predictors were mean-centered prior to analysis to minimize potential multicollinearity. Bivariate correlations were inspected to ensure minimal dependence among the predictors ($r < 0.42$), and residuals were examined to confirm the assumption of linearity in the logit. I tested the model for goodness-of-fit and confirmed it adequately described the observed outcomes in the data (Hosmer-Lemeshow statistic; $\hat{C} = 5.4$, $P = 0.7$).

To estimate the probability of recolonization at Picher Canyon, I used the specific values of conditions at Picher Canyon as parameter values in the predictive model. The resulting predictions are independent of the nesting history at Picher Canyon, because the abandoned colony sites used to develop the model did not include Picher Canyon.

RESULTS AND DISCUSSION

Regional reuse, abandonment, and recolonization of colony sites

Fifty-four Great Egret colonies were active in the northern San Francisco Bay area for one or more years, 1991-2011; on average, 21±0.8 (SE) colonies were active each year. Over all sites and years (n=418), active Great Egret colonies continued to be used in the next year 366 times. The overall regional, percent probability that colony sites would remain active in the next year was 87.6±1.6% (Figure 1). Great Egrets established colonies at new sites 32 times, suggesting the probability of 7.6±1.3% that new sites would be colonized over all sites and years. Colony sites were abandoned by Great Egrets 49 times, reflecting a regional percent probability of abandonment of 11.7±1.5% over all sites and years. Abandoned sites were recolonized 21 times, reflecting a rate of recolonization of 5.0 ±1.1% over all sites and years.

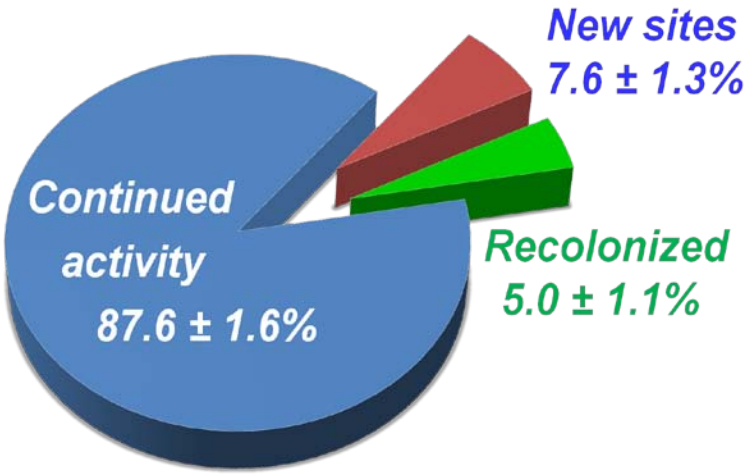

Figure 1. Percent of Great Egret nesting colonies established at colony sites that were active in the previous nesting season, at new colony sites, and at previously abandoned (recolonized) colony sites in the northern San Francisco Bay area, 1991-2011.

The regional percent use of recolonized sites depends on sites that have been abandoned for at least 13 years (recolonized in the 14th year), as indicated by the percent of recolonized sites in the region within subsets defined by increasingly larger periods of abandonment (Figure 2). Although we did not observe recolonization events after more than 13 years of abandonment, the limited extent of available data suggests that the actual length of time over which abandoned colonies provide viable opportunities for recolonization could be longer. Great Egrets recolonized 21 of 49 abandoned colony sites over the 21 year monitoring period, suggesting *eventual* recolonization at 42.0±7.14% of sites based on the limited extent of available data.

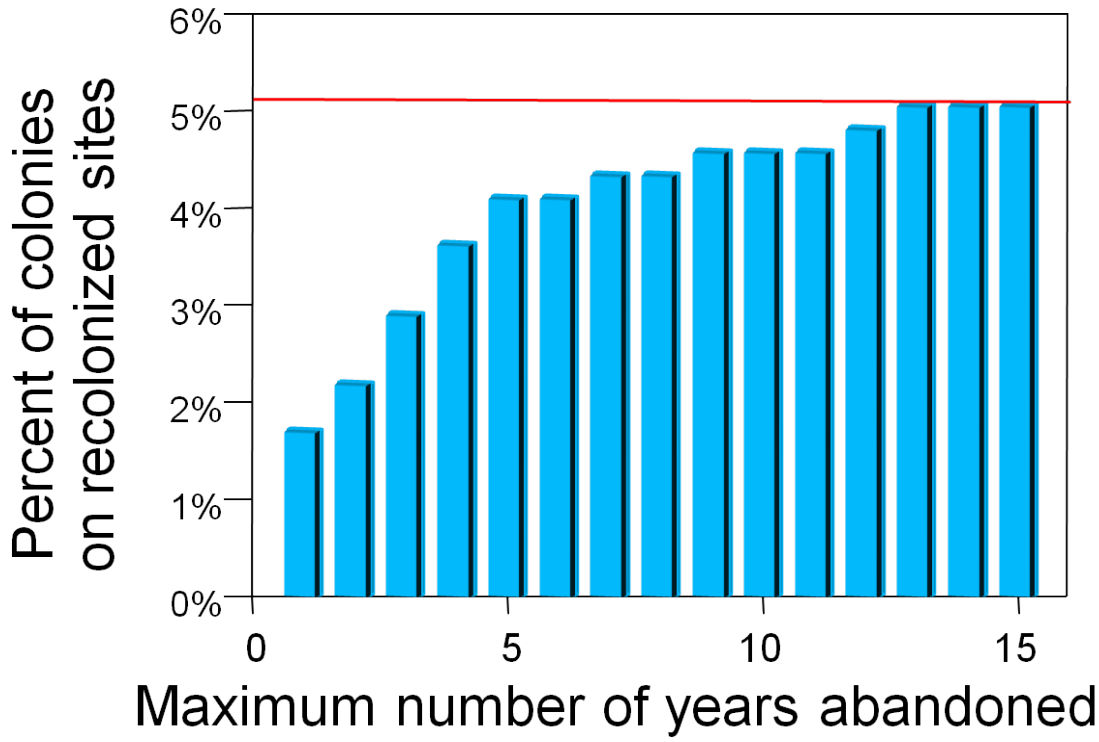

Figure 2. Cumulative percent recolonization by Great Egrets at sites recolonized within increasing periods of abandonment in the northern San Francisco Bay area, 1991 -2011; bars represent percent recolonization within cumulative subsets of available sites; each subset includes sites abandoned for one year up to the indicated maximum number of years. Regionwide use of colony sites (5.0 ±1.1%; horizontal red line) includes sites recolonized up to 13 years after abandonment.

Recolonization Probability

The best-performing model suggested that the probability of recolonization increases with the historic size of the nesting colony, the presence of other nesting heron or egret species, and the number of Great Egret nests immediately prior to abandonment (Table 1). The odds of recolonization were predicted to decline by about 10% , relative to the previous year (multiplied by 0.90), with each successive year after abandonment, and by over half (multiplied by 0.42) with each unit increase in classified level of human activity. None of the other candidate variables substantially influenced the likelihood of recolonization. The analysis was

based on 21 recolonization events across 280 abandoned-site-years. Although the results were highly significant, providing far better predictions than random chance ($P < 0.006$), they accounted for only 28% of the overall variation among abandoned sites and recolonization events in the region and should therefore be interpreted very cautiously ($R^2 = 0.28$).

Table 1. Logistic regression of the recolonization by Great Egret, based on the use of previously occupied colony sites in the northern San Francisco Bay area, 1991-2011 ($n = 264$, $R^2 = 0.28$, $P < 0.006$).

Independent predictor variable	Coefficient[a]	Odds[b]	SE	95% confidence Interval	
Human activity (levels 1-4)	−0.863	0.42	0.229	0.146	1.222[c]
Number of years abandoned (years)	−0.108	0.90	0.084	0.747	1.079[c]
Maximum known size of the Great Egret colony (number of nests)	0.015	1.01	0.009	0.997	1.032
Presence of other species prior to recolonization (presence/absence)	4.795	120.95	198.979	4.812	3040.431
Number of Great Egret nests in the year prior to abandonment (number of nests)	0.043	1.04	0.026	0.994	1.097
Constant	−2.140	0.12	0.043	0.058	0.240

[a]The predictive equation for the probability of recolonization is:

$\hat{p} = \exp(-2.140 + -0.8639 * \text{Human activity} + 4.795 * \text{Presence of other species} + 0.015 * \text{Maximum colony size} + 0.043 * \text{Great Egret nests prior to abandonment}) / [1 + \exp(-2.140 + -0.8639 * \text{Human activity} + 4.795 * \text{Presence of other species} + 0.015 * \text{Maximum colony size} + 0.043 * \text{Great Egret nests prior to abandonment})]$.

[b]The odds of recolonization change by this factor (multiplicatively) with each unit increase in the predictor variable; odds = (probability of recolonization)/(probability of no recolonization); odds of recolonization increase with the increases in the predictor if odds>1 and decrease if odds<1.

[c]Declining probability of recolonization (odds<1) with increasing human use is associated with an 89% level of confidence; declining probability with the increasing years of abandonment is associated with a 75% level of confidence.

Recolonization of Picher Canyon

Coefficients from the logistic model were used to predict the recolonization probability at Picher Canyon (Table 1). The results predicted about a 16% chance of a recolonization at Picher Canyon in the first year after abandonment, declining to less than 1.5% after 25 years of abandonment, if human activity is managed as a remote, rural site (Figure 3). If no nests are established in 2014, the "first year after abandonment" would be 2015, since egrets nested in the Canyon in 2013.

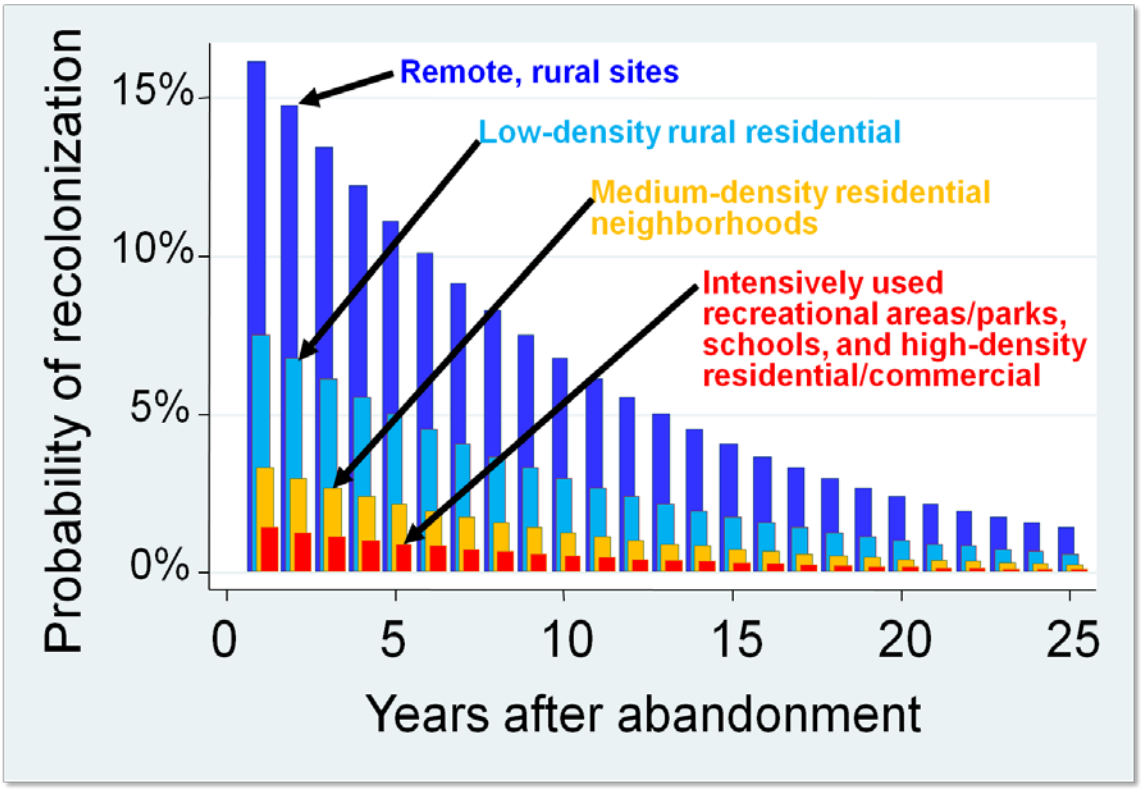

Figure 3. Predicted annual probability of recolonization at Picher Canyon by Great Egrets after abandonment, based on recolonization rates in the northern San Francisco Bay area, 1991-2011. Colors represent predictions associated with varying levels of human activity.

The analysis of cumulative probabilities of a future event over extended periods of time can provide a helpful planning tool in managing for rare occurrences subject to chance. Although the annual probability of recolonization declines over time, the cumulative probability of recolonization is additive across future year spans. Therefore, the sum of decreasing probabilities (Figure 3) results in an increasingly higher probability of future recolonization over longer periods of time (Figure 4). For example, although the predicted chance of recolonization declines to less than 1.5% after 25 years of abandonment (Figure 3), recolonization is predicted to occur within nine years after abandonment if the site is managed as a remote, natural area (Figure 4). The chance of recolonization is predicted to exceed 50% over time spans greater ten years after abandonment if human activity is managed at a level consistent with "low-density rural residential" conditions (Figure 4).

The results suggest the potentially important role of management in determining recolonization potential. For example, the (cumulative) probability of recolonization is predicted to range between 6% and 67% within five years after abandonment, depending on the level of human activity in the Canyon (Figure 4). These results are consistent with the management approach recommended in the Picher Canyon Management Framework (Millus et al. 2013). The Framework identified the potential value of minimizing levels of human activity to avoid deterring individual egrets in their annual selection of new colony sites. Increases in the chance of future recolonization over extended periods of time, as described

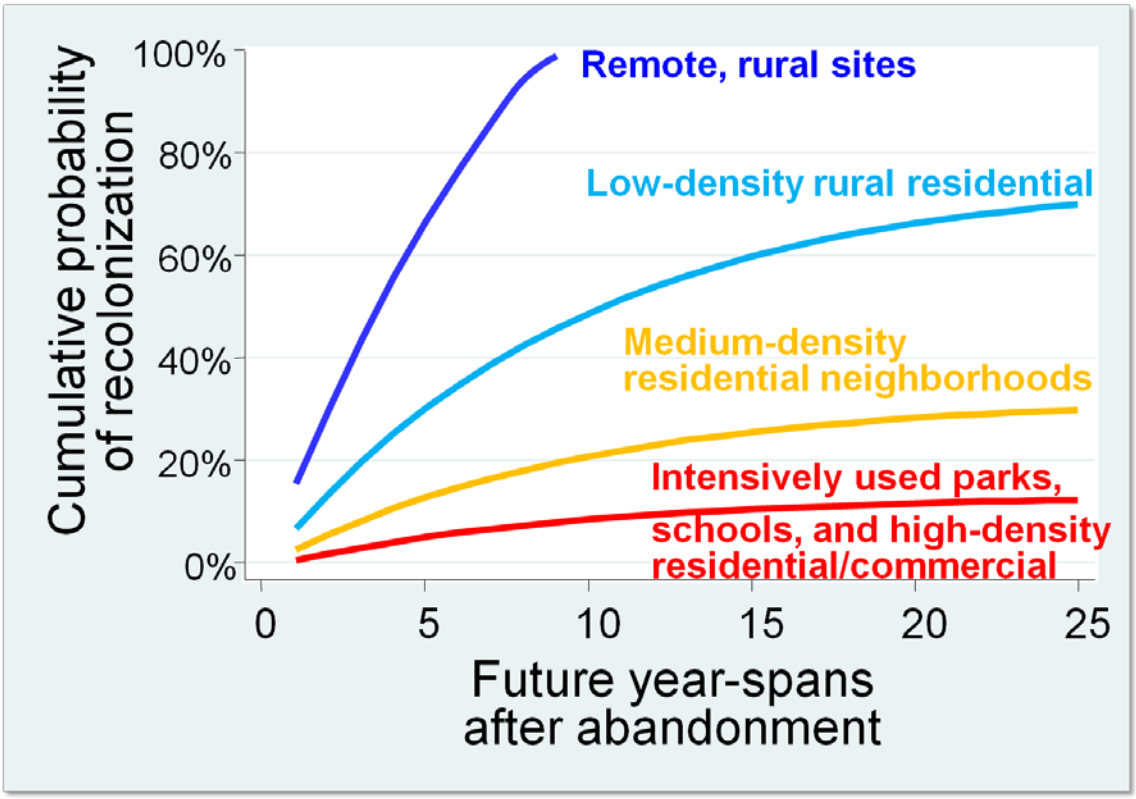

Figure 4. Predicted cumulative probability of recolonization at Picher Canyon by Great Egrets over increasing future year spans after abandonment. The results are based on modeled recolonization probabilities among of abandoned sites in the northern San Francisco Bay area, 1991-2011, and on the particular conditions at Picher Canyon. Colors represent predictions associated with varying levels of human activity.

in this analysis, are consistent with the results of other ACR research: annual rates of growth in nest abundance within subregional wetland areas such as Bolinas Lagoon are expected to fall below normal background growth rates for several years after a major colony-site decline (Millus and Kelly, in preparation).

Uncertainty is a fundamental aspect of natural areas management. Therefore, the management of natural areas can rarely, if ever, guarantee particular outcomes. The results presented here suggest a potentially compelling probability of recolonization at Picher Canyon over time. However, the predictions are best understood as probabilistic, based on underlying variability subject to chance—"heads" is accurately predicted, on average, within two flips of a coin, but other outcomes often occur. Changes in regional population size, nesting distribution, the quality of surrounding feeding areas, or other complex ecological influences that drive the nesting behaviors of herons and egrets, could result in a dramatic recolonization of the heronry at any time or, alternatively, continuing avoidance. Because the behaviors of herons and egrets are often mysterious and unpredictable, exactly when or if Great Egrets will recolonize Picher Canyon remains unknown.

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