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Nesting Dynamics of Four Ardeid Species at Subregional Scales: Recovery Rates after Sudden Major Declines in Nest Abundance

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Abstract.—The functional roles of nesting heron species (Ardeidae) as top predators in regional wetland landscapes may be sensitive to variation in nesting abundances at subregional scales corresponding to available habitat for nesting and foraging within individual wetland subsystems. This study investigates the dynamics of annual nesting abundances of four ardeid species within 10 major wetland subsystems of the San Francisco Bay Area, California, USA, during 1991-2010. Interrupted time series analysis was used to measure impact and recovery rates related to sudden major declines in nesting abundance below selected thresholds of annual change. Year-to-year persistence of initial impacts was above 78% for Great Blue Herons (*Ardea herodias*) and Great Egrets (*A. alba*). Snowy Egrets (*Egretta thula*) recovered more quickly, with 63-66% annual carryover of initial impacts. The time required for 95% recovery averaged 18.8 years for Great Blue Heron, 13.0 years for Great Egret, 7.2 years for Snowy Egret, and 14.5 years for Black-crowned Night-Heron (*Nycticorax nycticorax*). Most of the major subregional declines in nest abundance were associated with impacts at a single colony site. The results highlight the significant effects of sudden major declines in nesting abundance on the status of ardeids within individual wetland systems across a larger regional wetland landscape. *Received 5 February 2018, accepted 26 May 2018.*

Key words.—Ardeidae, colonial, disturbance, foraging range, landscape, management scale, nesting distribution, recovery, subregion, time series.

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Understanding ecological relationships requires investigation at appropriate spatial and temporal scales relative to the questions addressed and the "ecological neighborhood" of the associated organisms (Addicott *et al.* 1987; Wiens 1989). Although predicted recovery rates after major disturbance are a key aspect of environmental planning, models are lacking to predict the recovery of heron species' (Ardeidae) nest abundances at spatial scales corresponding to the availability of resources for both nesting and foraging. The effective conservation of ardeids and their functional influence as top predators in extensive wetland complexes suggests the importance of understanding the impacts of disturbance and the associated recovery of nesting and foraging densities at subregional scales, which are likely to reflect differences in wetland condition, access to foraging areas, and the corresponding use of colony sites (Pratt 1983; Kelly *et al.* 2007; Kelly and Nur 2015). The status of nesting ardeids at subregional scales may not be reflected by their status or dynamics in the surrounding region because processes operating at larger spatial scales can mask the changes occurring at smaller spatial scales (Wiens 1989; Schneider 1994). Similarly, the dynamics of individual nesting colonies can be averaged out over larger spatial scales and often fail to reflect annual changes within a subregion.

Nesting ardeids respond to environmental changes beyond the immediate vicinity of their colony sites. Patterns of colony-site selection and reproductive success in ardeids reflect adaptive responses to surrounding landscape conditions within their foraging range (Fasola *et al.* 2002; Custer *et al.* 2004; Kelly *et al.* 2008; Baker *et al.* 2015). Colony-site occupancy can vary substantially in response to changes in extent and/or quality of their wetland feeding areas (Bancroft *et al.* 1994; Tourenq *et al.* 2000; Kelly *et al.* 2008; Carrasco *et al.* 2015), disturbance by potential nest predators (Post 1990; Kelly *et al.* 2005; Kenyon *et al.* 2007), disturbance or interference associated with nearby human activities (Tremblay and Ellison 1979; Rodgers and Smith 1995; Hafner 2000), heavy rainfall (Hafner *et al.* 2001; Kelly and Condeso 2014), or catastrophic events such as hurricanes (Shepherd *et al.* 1991; Raynor *et al.* 2013).

Because nesting ardeids generally forage within a few to 10 km of nest sites (Custer *et al.* 2004; Kelly *et al.* 2008; Manikowska-Ślepowrońska *et al.* 2016), individual wetland systems or subsystems within a regional wetland complex often provide reasonable units for management corresponding to both the foraging movements of nesting herons and egrets and to the scales of hydrologic connectivity that distinguish wetland landscapes (Haig *et al.* 1998). The effective conservation of wetland landscapes depends on the consideration of processes and issues at such intermediate (hereafter, "subregional") scales associated with particular wetland types or systems such as estuaries, delta marshes, lagoons, wetland basins, and watersheds (Turner *et al.* 2000). However, little is known about the long-term dynamics of ardeid nest abundances at such scales.

Ardeid individuals may readily abandon their nest attempts and can exhibit low levels of breeding-site fidelity in response to changes in habitat conditions at a colony site or across the surrounding wetland landscape (Frederick and Collopy 1989; Melvin *et al.* 1999; Kelly *et al.* 2008; Carrasco *et al.* 2017). After nest failure, or between nesting years, herons and egrets may select new nest locations in a different wetland subregion within the larger regional landscape or, unless isolated by considerable distances, may relocate to another wetland region (Fasola *et al.* 2002; Kelly and Condeso 2014; Galarza *et al.* 2016). Major disturbance leading to nest failure or abandonment at one or more colony sites within a subregion may not affect subregional nesting abundances if most of the affected individuals establish new nests within the same colony or at another nearby colony site. However, larger shifts in colony-site selection by nesting ardeids, including spatial shifts in the recruitment of first-time breeders, are likely to result in dynamic changes in nesting distribution among subregions (Bancroft *et al.* 1994; Fasola *et al.* 2002; Kelly *et al.* 2007; Santoro *et al.* 2016). Because ardeids tend to nest within accessible range of foraging sites, such changes are likely to result in correlated changes in subregional foraging densities (Bancroft *et al.* 1994; Custer *et al.* 2004; Kelly *et al.* 2008).

If a major nesting decline results from the degradation or loss of foraging habitat, the time to recovery is likely to depend on the restoration or resilience of suitable habitat or available prey (Bancroft *et al.* 1994; Fasola *et al.* 2010; Rush *et al.* 2015; Klassen *et al.* 2016), whereas the recovery from major declines in nest abundance associated with disturbance to colony sites (e.g., by potential nest predators or human activity) may depend on rates of colonization or recruitment inherent to the surrounding population. If nest disturbance leads to a subregional decline in nesting abundance while foraging conditions remain relatively stable, the recovery of nest numbers might be facilitated by improved foraging opportunities related to a reduction of density-dependent constraints and enhanced recruitment of adults or first-time breeders from other areas (Gill and Mewaldt 1979; Melvin *et al.* 1999; Fasola *et al.* 2002; Shirai 2013). However, the extent to which density-dependent foraging affects heron and egret nest abundances is not clearly understood (Butler 1994; Shirai 2013; Kelly and Condeso 2014).

San Francisco Bay and the adjacent Central Valley of California, USA, have been recognized as a region of hemispheric importance to ardeids in North America, with critical value to heron species conservation in the Pacific Flyway (Butler *et al.* 2000). Our objectives were to determine the extent to which sudden major subregional declines in annual nesting abundance below selected thresholds of annual change, within wetland subregions of the northern San Francisco Bay Area, affect the future abundances of four ardeid species: Great Blue Heron (*Ardea herodias*), Great Egret (*A. alba*), Snowy Egret (*Egretta thula*), and Black-crowned Night-Heron (*Nycticorax nycticorax*).

Methods

Study Area

The study area includes a set of 10 subregional wetland landscapes within approximately 9,950 km^2 of the northern San Francisco Bay Area, California, USA (Fig. 1; Kelly *et al.* 2007). The southern portion of the study area extends across extensive tidal marshes and seasonal wetlands of the San Francisco Estuary; the northern portion includes the hillsides and lower slopes of the coastal mountains. Each of the 10 subregional areas was defined by an associated major wetland system with suitable habitat for foraging herons and egrets, distinguished by watershed boundaries and large areas of open water considered unsuitable for foraging. We used the California Aquatic Resource Inventory (San Francisco Estuary Institute 2016) to approximate the boundary and areal extent of the central "core wetland system" (mean = 51.0 ± 25.2 km^2 [SE]) in each subregion (Table 1); these boundaries were used to determine which nesting colonies were established within an accessible distance to each system, based on the foraging ranges of our study species. Nesting colonies within 10 km of each core wetland system were assumed to be within foraging range of the associated core wetlands and grouped

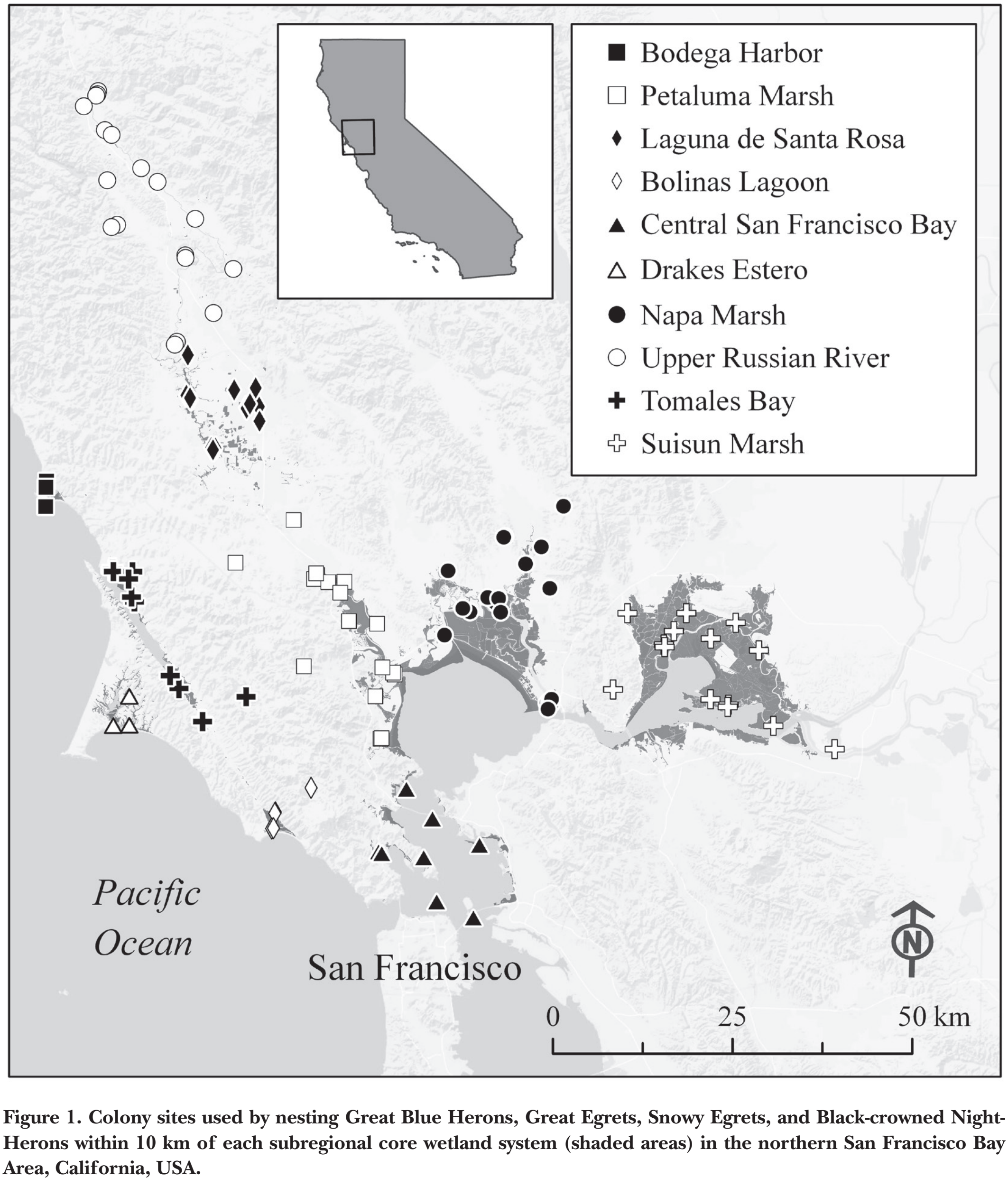

Figure 1. Colony sites used by nesting Great Blue Herons, Great Egrets, Snowy Egrets, and Black-crowned Night-Herons within 10 km of each subregional core wetland system (shaded areas) in the northern San Francisco Bay Area, California, USA.

Table 1. Wetland subregions in the northern San Francisco Bay Area, California, USA, the areal extent of the core wetland habitat considered suitable for foraging by ardeids in each subregion (San Francisco Estuary Institute 2016), and the areal extent of the associated landscape within 10 km of the core wetlands (Fig. 1).

Wetland Subregion	Core Wetland Area (km^2)	Subregional Area (km^2)
Laguna de Santa Rosa	20.7	1,499
Petaluma Marsh	53.1	1,177
Napa Marsh	129.6	1,342
Suisun Marsh	249.2	1,947
Central San Francisco Bay	12.8	1,298
Tomales Bay	11.7	1,222
Bolinas Lagoon	4.7	497
Bodega Harbor	2.4	481
Drakes Estero	10.9	699
Upper Russian River	2.2	1,426

to facilitate analysis of subregional nesting abundances (Custer and Osborn 1978; Hoefler 1980; Custer *et al.* 2004; Kelly *et al.* 2008; Table 1; Fig. 1). Only a few colony sites were within 10 km of two or more core wetland systems; these sites were assigned to the subregion with the nearest core wetland habitat suitable for foraging.

Only wetland types that were potentially suitable for foraging were included in the core area measurements; large areas of open water and other unsuitable habitat were excluded. The inclusion of suitable foraging habitat was based on the presence of emergent wetland vegetation or water depths below 30 cm (Gawlik 2002; Kelly *et al.* 2008; San Francisco Estuary Institute 2016; J. P. Kelly and T. E. Condeso, pers. obs.). Patches of potentially suitable wetland habitat that were very small (< 1 ha) and isolated by more than 100 m of upland were excluded because they contribute only a trivial amount to the area of each core wetland, were not considered to be functionally contiguous to the core wetland system, and, by expanding the 10-km boundary of each core wetland, would lead to the overlap of adjacent wetland subregions and confusion in assigning colony sites to the most accessible wetland system.

The core wetlands within subregions were characterized by extensive tidal marshes, coastal lagoons, freshwater depressional wetlands, seeps and springs, vernal pools, and historic wetlands that have been diked and drained, managed as marshes or ponds for flood control or waterfowl hunting, or restored to tidal action (San Francisco Bay Area Wetlands Ecosystem Goals Project 1999). We also included the edges (10 m wide) of large, deep lakes and the Russian River, the dominant riverine feature on this landscape. The surrounding subregional landscapes included isolated patches of seasonal wetlands, vernal wetlands, farm ponds, reservoirs, creeks, urban and suburban areas, riparian and upland forests, scrublands, and grazed or cultivated uplands.

The annual percent of nests established by our study species in colony sites used by one or more other heron species was particularly consistent over the 20-year study period, representing 53.1 ± 1.62%, 97.7 ± 1.25%, 100.0 ± 0.00%, and 74.7 ± 6.37%, respectively, of Great Blue Heron, Great Egret, Snowy Egret, and Black-crowned Night-Heron nests in the northern San Francisco Bay Area. In this study, we focus on the dynamics of species' nesting abundances at subregional scales; further investigation would be needed to evaluate the potential influence of nesting dynamics at the colony-site scale, including the relative use of mixed colony sites (Kelly *et al.* 2007). Colonial-nesting ardeids in the study area are represented primarily by our study species. Green Herons (*Butorides virescens*) nest along streams throughout the region but do not occur at colony sites used by our study species; Cattle Egrets (*Bubulcus ibis*) nest at only one colony site and were excluded from the analysis.

Surveys and Monitoring

The locations of all known colony sites in the study region (1991-2010; 57 ± 1.1 active sites/year) were determined using a variety of resources and techniques. Although it is impossible to fully confirm the absence of new colonies that may not have been observed, we are confident that subregional nest abundances were estimated with a high level of accuracy. Our confidence is supported by: 1) aerial and intensive ground-based searches for all existing colony sites in 1991; 2) annual searches for new colony sites throughout the region during the post-guardian period (May and June), when colony sites are most conspicuous because both adults at each nest are provisioning nestlings, nestlings are often large enough to be easily seen or heard, and guano accumulations are visible beneath nests; 3) aerial surveys in selected subregions in 2004 and 2005 (Laguna de Santa Rosa, Central San Francisco Bay, and Suisun Marsh; Fig. 1); 4) monthly, or more frequent, regional observations by 60-90 trained volunteer field observers each year who contributed directly to this project; 5) focused, subregional efforts to detect new colony sites whenever local sites were abandoned; 6) regular, ongoing communications with State, regional and local natural resources agencies, land managers, and birding networks; and 7) ongoing communications with county breeding bird atlas coordinators and contributors, collectively including field observations from 37 county-atlas years across all five counties in the study area. In addition, the detection of newly established colony sites did not significantly influence the estimated impact recovery rates within subregions: the time-series models described below included a preliminary predictor associated with the cumulative effects, at each time step, of 45 newly established colony sites detected during the course of this study, but it did not significantly affect the estimated changes in annual nesting abundance and was subsequently dropped from the models (*t*-tests; Great Blue Heron: $t_{370} = 1.11$, $P > 0.27$; Great Egret: $t_{196} = 0.50$, $P > 0.62$; Snowy Egret: $t_{196} = 0.11$, $P > 0.91$; Black-crowned Night-Heron: $t_{196} = 0.26$, $P > 0.80$).

Most colony sites were visited at least four times each breeding season, generally at monthly or more frequent intervals. Sites that could be visited only once in a given year (13.0 ± 0.7%/year) were observed in May or early June when nesting birds were conspicuous and observations were likely to provide a close estimate of peak nest abundance. We estimated annual nest abundances by summing the peak number of active nests at each colony site across the colony sites in each wetland subregion. Nest survivorship and evidence of nesting disturbance were also assessed annually at each colony site. Detailed field methods are described in Kelly *et al.* (2007).

Statistical Analysis

To evaluate the effects of sudden major declines in nesting activity on future nest abundances, we analyzed up to 10 20-year time series, by species, across the associated panel of 10 wetland subregions (Table 1). Some species did not nest every year in every subregion, and all time series began with > 0 nests. All time series were at least 10 years in length (Table 2); to avoid potentially imprecise estimates of subregional nesting dynamics, we excluded two Black-crowned Night-Heron time series that were only 2 and 3 years in length). Time series for nesting Great Blue Herons and Great Egrets were evaluated across all 10 subregions; those for nesting Snowy Egrets and Black-crowned Night-Herons were limited to seven and six subregions, respectively. We used first-order autoregressions involving interrupted time series analysis across a panel of wetland subregions to estimate the extent to which sudden major declines in annual nest abundance affect the subregional growth of nest abundances in each of our study species (McDowall *et al.* 1980; Bisgaard and Kulahci 2011; Box *et al.* 2016). This approach accounts for underlying trends and stochastic components of the time series to estimate impact and recovery rates that exceed the null condition of normal background dynamics in the system.

We defined thresholds of sudden major decline as changes in annual $\log_e$ nest abundance that drop below 80%, 90%, or 95% of the annual variation within species and subregions. Therefore, each threshold of sudden major decline is proportional to expected levels of annual variation, which may differ among species with different nesting dynamics and, possibly, among subregions that differ in expected levels of human activity, potential nest predators, or other factors that affect variation in subregional nest numbers. To interpret the standardized levels of impact and response as

Table 2. Length of time series in years (*n*) for species' nest abundances in each wetland subregion in the northern San Francisco Bay Area, California, USA, and the number of years when nest abundance dropped below thresholds for sudden major decline, based on the lower 0.80, 0.90, and 0.95 quantiles of the standard normal variation in annual nest abundance.

	Great Blue Heron				Great Egret				Snowy Egret				Black-crowned Night-Heron			
Subregion	*n*	0.80	0.90	0.95	*n*	0.80	0.90	0.95	*n*	0.80	0.90	0.95	*n*	0.80	0.90	0.95
Bodega Harbor	20	6	3	3	20	2	1	0	11	1	0	0	20	0	0	0
Bolinas Lagoon	20	2	1	1	20	0	0	0	20	1	1	1	0	–	–	–
Central San Francisco Bay	20	0	0	0	20	2	0	0	20	1	0	0	20	0	0	0
Drakes Estero	16	3	1	1	16	1	1	1	0	–	–	–	0	–	–	–
Laguna de Santa Rosa	20	1	0	0	20	1	0	0	19	1	0	0	20	2	1	1
Napa Marsh	20	2	2	1	19	1	0	0	19	0	0	0	20	3	1	0
Petaluma Marsh	20	4	2	1	19	0	0	0	20	1	0	0	20	3	3	2
Suisun Marsh	20	3	2	2	20	1	1	0	17	1	0	0	2	–	–	–
Tomales Bay	20	1	0	0	20	0	0	0	0	–	–	–	10	2	1	0
Upper Russian River	20	6	2	0	14	0	0	0	0	–	–	–	3	–	–	–

percent change, we back-transformed the observed and predicted changes in $\log_e$ nest abundance. With this approach, we let $Y_{i,t}$ represent the $\log_e$ nest abundance in subregion i in year t, and considered it to be an independent, normally and identically distributed variable with parameters μ_i and σ_i such that $\mu_i = \mathrm{E}(Y_i)$ and $\sigma^2_i = \mathrm{var}(Y_i)$. Thresholds for sudden major decline were defined as the lower 0.80, 0.90, and 0.95 quantiles of a standard normal variable ($Z_{0.80} = -0.842$; $Z_{0.95} = -1.6495$, and $Z_{0.90} = -1.282$ standard deviations below the mean, respectively). To fully capture the standard probabilities of changes in annual nest abundance, thresholds used to identify years with sudden major declines in nest abundance were based on the means of 1,000 bootstrap samples of the time series for each species within each subregion. Years with sudden major declines were modeled as annual binary indicators at each threshold level.

Preliminary autoregressive models were used to account for the underlying density-dependent dynamics of the system during years without sudden major declines in nest abundance. For each species, we set X_t as the $\log_e$ nest abundance in subregion i ($X_i = \ln[x_i+1]$) in the current ($X_{i,t}$) or previous ($X_{i,t-1}$) year:

$$X_{i,t} = a_0 + (a_1)\ X_{i,t-1} + \varepsilon_{i,t}\ ,$$

where a_0 is the intrinsic rate of increase in nest abundance without density dependence, α_1 is the strength of direct (first-order) density dependence, and $\varepsilon_{i,t}$ is the residual variation in subregional nest abundance. These models assume a linear relationship between realized annual growth and the natural log of nest abundance in the prior year. We verified that the autoregressive components of the models effectively identified and controlled for the underlying background variation and trends in the system, generating residuals ($\varepsilon_{i,t}$) that were stationary (not autocorrelated, with a mean of zero and constant variation over time) within subregions and across panels using Dickey-Fuller unit-root tests ($P < 0.05$; StataCorp 2013), with no cross-sectional dependence among wetland subregions (Pesaran tests, $P > 0.05$; Pesaran 2004).

The resulting parameters in the preliminary models are then applied to the full time series for each species (across all years, with and without major declines in nest abundance) to account for the expected, normal background dynamics of the system and to isolate, in the model residuals, changes that exceed the underlying background variation. The residuals become the impact-recovery time series ($y_{i,t}$) used to estimate responses to sudden major declines in nest abundance (McDowall *et al.* 1980). As in the preliminary models, the results were substantiated by confirming the model assumptions that the residuals ($\varepsilon_{i,t}$) of the $y_{i,t}$ time-series models were stationary and not autocorrelated, with a mean of zero and a constant variance over time, within subregions and across panels (Dickey-Fuller unit-root tests for cross-sectional data, $P < 0.05$; StataCorp 2013), and that there was no cross-sectional dependence among wetland subregions (Pesaran tests, $P > 0.05$). The impact-recovery time series is modeled as:

$$y_{i,t} = (\hat{\delta})\ y_{i,t-1} + (\hat{\omega})\ D_{d,i,t}\ ,$$

where $\hat{\omega}$ is the sudden major decline in $\log_e$ nest abundance during years that exceed the threshold level d = 0.80, 0.90, or 0.95 associated with a value of "1" in the indicator variable $D_{d,i,t}$ (otherwise coded as zero), and $\hat{\delta}$ is the estimated annual carryover (persistence) of the initial impact of sudden major decline in nest abundance (annual rate of decay of the effect); $1-\hat{\delta}$ estimates the annual rate of recovery. The estimated changes in subregional nest abundance are measured as responses to sudden major declines followed by gradual recovery to a stable growth rate of zero (relative to other underlying trends). All statistical analyses were conducted using Stata (StataCorp 2013).

The analysis does not investigate potential mechanisms that account for the observed impact and recovery rates. The autoregressive components of the models control for the prior dynamics and underlying trends in each wetland subregion and, consequently, also control for any correlated changes across the panel of subregions. Therefore, the estimated impacts and recovery rates are independent of inter-year movements by nesting adults between subregions. In addition, the predicted recovery rates are independent of the expected rates of natal dispersal and recruitment of first-time breeders from other areas. Therefore, the analysis makes no assumptions about underlying trends in nest abundance or whether the observed subregional dynamics operate as closed systems.

Time-invariant differences between neighboring subregions, including the apparently consistent subregional extent of core-wetlands over the duration of the study period, are perfectly collinear with modeled differences across the panel of wetland subregions (intraclass correlation [rho] = 1.0; cross-panel differences account for 100% of the variance); thus, differences in the extent of core wetlands are included in the modeled differences among subregions and omitted automatically from the models. Therefore, we examined post-hoc correlations between the estimated species recovery rates and the extent of core wetlands in each subregion.

The residual impact (reduced rate of annual growth), n years after a sudden major decline in nest abundance in year t, can be estimated as:

$$y_{t+n} = \hat{\delta}^{n}\,\hat{\omega}$$

where $\hat{\delta}^{n}$ is the proportional effect of the original impact in year $t + n$ and $1-\hat{\delta}^{n}$ is the proportional extent of recovery (McDowall *et al.* 1980). Thus, the number of years to 95% recovery from the original impact is $n = \ln(0.05)/\ln(\hat{\delta})$. The residual impact of multiple years with sudden major declines in nest abundance at different predicted levels of proportional impact ($\hat{\omega}$) n years after each of i events can be estimated as:

$$y_{t+n} = \hat{\delta}_1^{n_1}\,\hat{\omega}_1 + \hat{\delta}_2^{n_2}\,\hat{\omega}_2 + \ldots\ \ldots + \hat{\delta}_i^{n\,i}\,\hat{\omega}_i\ .$$

Model results were back-transformed to illustrate predicted rates of recovery as percent change. We estimated the percent of major subregional declines in nest abundance that was associated with disturbance at a single colony site based on the occurrence of comparable declines at particular colony sites resulting from observed or inferred nesting disturbance.

Results

Peak nest abundance varied considerably among subregions for all species (Table 3). The number of years with sudden major declines in nest abundance exceeding each threshold level, pooled across subregions, ranged from 1-28 years (Table 4). Observed responses to sudden major declines in subregional nest abundance varied considerably among species (Fig. 2). During our 20-year period of study, Great Blue Herons experienced a substantially higher frequency of years with sudden major declines than other species, with significantly lower initial impacts ($\hat{\omega}$) at all threshold levels (Table 4), suggesting that this species is subject to relatively frequent, but less intense disturbances than other species.

The estimated annual persistence of impacts imposed by sudden major declines in nest abundance ($\hat{\delta}$) is similar within species, suggesting that annual rates of recovery are generally consistent across levels of impact (Table 4). Therefore, from this point forward (unless noted otherwise), we focus on responses to all sudden major declines in nest abundance exceeding the minimum 0.80 threshold of initial impact, which maximizes sampling strength because this threshold includes the nested responses at the 0.90 and 0.95 levels of impact. The time-series models generated significant, stable estimates of impact and recovery rates for all study species, accounting for nearly all differences between subregions ($R^2 > 0.96$) and considerable proportions of variation within subregions (Great Blue Heron: $R^2 = 0.68$, $F_{2,174} = 186$, $P < 0.0001$; Great Egret: $R^2 = 0.76$, $F_{2,154} = 241$, $P < 0.0001$; Snowy Egret: $R^2 = 0.39$, $F_{2,90} = 29$, $P < 0.0001$; Black-crowned Night-Heron: $R^2 = 0.64$, $F_{2,82} = 76$, $P < 0.0001$).

The annual carryover rates ($\hat{\delta}$) of impacts associated with sudden major declines in nesting abundance were 85 ± 0.04% for Great

Table 3. Mean and standard error (SE) of subregional peak nest abundance of colonial ardeid species in wetland subregions of the northern San Francisco Bay Area, California, USA, 1991-2010 (*n* = 20).

	Great Blue Heron		Great Egret		Snowy Egret		Black-crowned Night-Heron	
Subregion	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Bodega Harbor	3.6	0.40	11.8	10.43	2.1	13.65	1.3	0.40
Bolinas Lagoon	13.0	0.96	77.2	2.20	4.1	0.76	0	–
Central San Francisco Bay	22.9	1.56	120.7	1.90	158.1	5.10	219.3	27.81
Drakes Estero	3.3	0.65	8.4	1.90	0	–	0	–
Laguna de Santa Rosa	41.4	1.86	55.4	5.26	34.9	16.87	85.1	11.09
Napa Marsh	121.1	10.14	24.2	5.59	106.8	1.71	122.1	9.86
Petaluma Marsh	20.4	1.81	22.1	0.48	10.4	0.92	39.2	4.25
Suisun Marsh	93.4	5.98	424.3	23.45	2.1	0.92	0.6	0.55
Tomales Bay	31.0	2.35	36.4	0.75	0	–	0.7	0.22
Upper Russian River	22.8	2.65	2.6	0.48	0	–	0.9	0.80
Total (all subregions)	372.9	12.72	783.1	27.03	318.5	22.41	469.2	31.83

Table 4. Results of interrupted time series models. The values presented for each species and impact threshold of sudden major decline in subregional nest abundance are number of observations across all subregions (*n*); number of wetland subregions (k); number of impact years; estimated annual rate of decay of the initial impact ($\hat{\delta}$ ± SE); estimated initial impact ($\hat{\omega}$ ± SE); percent change of estimated initial impact; and predicted years to 95% recovery with 95% confidence interval (CI). Asterisk (*) indicates the significance ($P < 0.001$) of coefficients for each parameter.

Species	*n*	k	Impact Years	$\hat{\delta}$ ± SE	$\hat{\omega}$ ± SE	Initial Impact (% Change)	Years to 95% Recovery	95% CI
0.80 impact threshold								
Great Blue Heron	176	10	28	0.85 ± 0.036*	-0.61 ± 0.056*	-45.7	18.8	9.0-28.7
Great Egret	156	10	8	0.79 ± 0.032*	-1.18 ± 0.143*	-69.3	13.0	8.6-17.4
Snowy Egret	90	7	6	0.66 ± 0.071*	-1.26 ± 0.285*	-71.6	7.2	3.6-10.9
Black-crowned Night-Heron	82	6	10	0.81 ± 0.054*	-1.13 ± 0.133*	-67.7	14.5	5.3-23.7
0.90 impact threshold								
Great Blue Heron	176	10	13	0.83 ± 0.039*	-0.68 ± 0.145*	-49.3	15.8	8.1-23.4
Great Egret	156	10	3	0.79 ± 0.033*	-1.96 ± 0.250*	-85.9	13.1	8.4-17.8
Snowy Egret	90	7	1	0.63 ± 0.077*	-1.32 ± 0.688*	-73.3	6.6	3.2-10.1
Black-crowned Night-Heron	82	6	6	0.76 ± 0.057*	-1.31 ± 0.182*	-73.0	11.0	5.1-17.0
0.95 impact threshold								
Great Blue Heron	176	10	9	0.78 ± 0.036*	-0.93 ± 0.094*	-60.1	12.1	7.7-16.6
Great Egret	156	10	1	0.79 ± 0.032*	-3.12 ± 0.339*	-95.6	13.0	8.6-17.5
Snowy Egret	90	7	1	0.64 ± 0.077*	-1.32 ± 0.688*	-73.3	6.6	3.2-10.1
Black-crowned Night-Heron	82	6	3	0.74 ± 0.063*	-1.66 ± 0.312*	-80.1	10.1	4.4-15.7

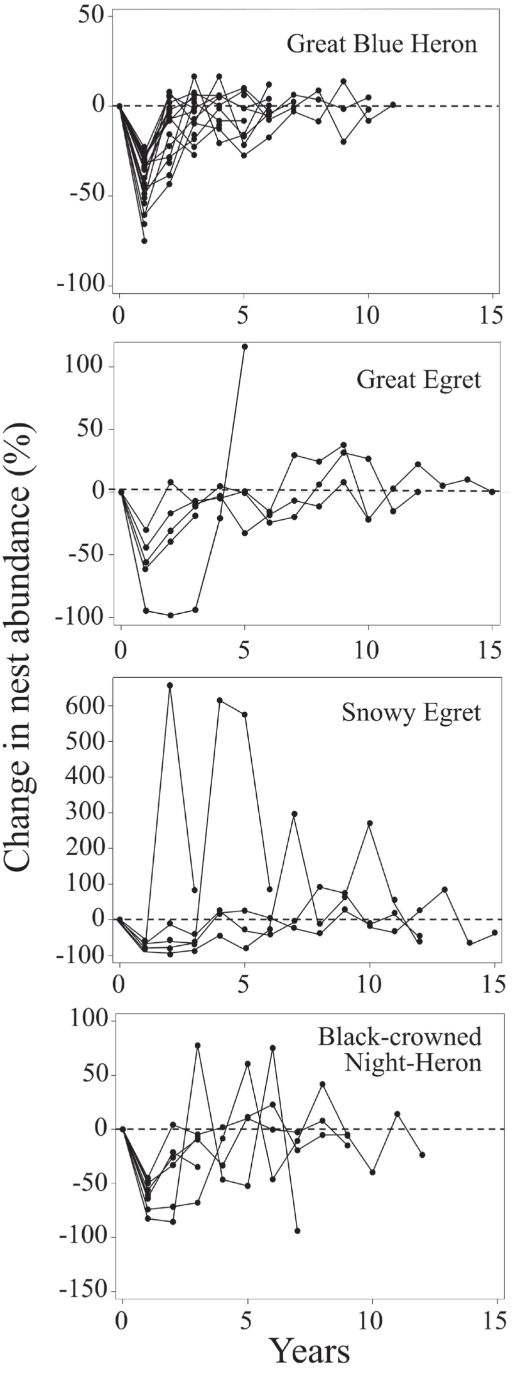

Figure 2. Observed values (filled circles) of sudden major decline in $\log_e$ nest abundances (falling below the lower 0.80 quantile of standard normal annual variation in Year 1) and associated recovery by four ardeid species, back-transformed to represent percent annual change. Solid lines connect the subsequent values of recovery within subregions of the northern San Francisco Bay Area, California, USA. Other underlying background dynamics and trends are controlled and reduced to zero (dashed line).

Blue Herons, 79 ± 0.03% for Great Egrets, 66 ± 0.07% for Snowy Egrets, and 81 ± 0.05% for Black-crowned Night-Herons (Table 4). Thus, Snowy Egrets exhibited the fastest annual recovery rates $(1-\hat{\delta})$ after years with sudden major declines (34 ± 0.07% / year). Great Blue Herons exhibited the slowest annual recovery rates (15 ± 0.04% / year), and intermediate rates of annual recovery were exhibited by Great Egrets (21 ± 0.03% / year) and Black-crowned Night-Herons (19 ± 0.05% / year). The predicted number of years needed for 95% recovery, relative to other underlying trends and dynamics, was 18.8 years for Great Blue Heron, 13.0 years for Great Egret, 7.2 years for Snowy Egret, and 14.5 years for Black-crowned Night-Heron, with 95% confidence intervals suggesting the possibility of substantially shorter or longer periods of recovery (Table 4; Figs. 3 and 4). Estimated recovery rates $(1-\hat{\delta})$ appeared to be faster in subregions with more extensive of core wetlands, when species differences were controlled (r = 0.37, P = 0.04, n = 32); however, the relationships were positive but not significant (P > 0.11) when calculated separately for each species (Great Blue Heron: r = 0.49, n = 10; Great Egret: r = 0.34, n = 10; Snowy Egret: r = 0.47, n = 6; Black-crowned Night Heron: r = 0.71, n = 6). Repeated sudden major declines in nest abundance at intervals shorter than the considerably long recovery times estimated by our results could result in ongoing depression or decline of growth rates over very long periods of time, relative to other underlying trends (Fig. 5).

Most of the major subregional declines in nest abundance (exceeding the 0.80 threshold of sudden decline) were associated with observed or inferred disturbance events at a single colony site, including instances of interference by nest predators, human activity, and impacts to nesting substrates (Great Blue Heron: 68 ± 9% of sudden major declines, n = 28; Great Egret: 88 ± 13%, n = 8; Snowy Egret: 67 ± 21%, n = 6; Black-crowned Night-Heron: 100%, n = 10). We were unable to determine the relative importance of colony-site disturbance resulting from human activity vs. potential nest predators.

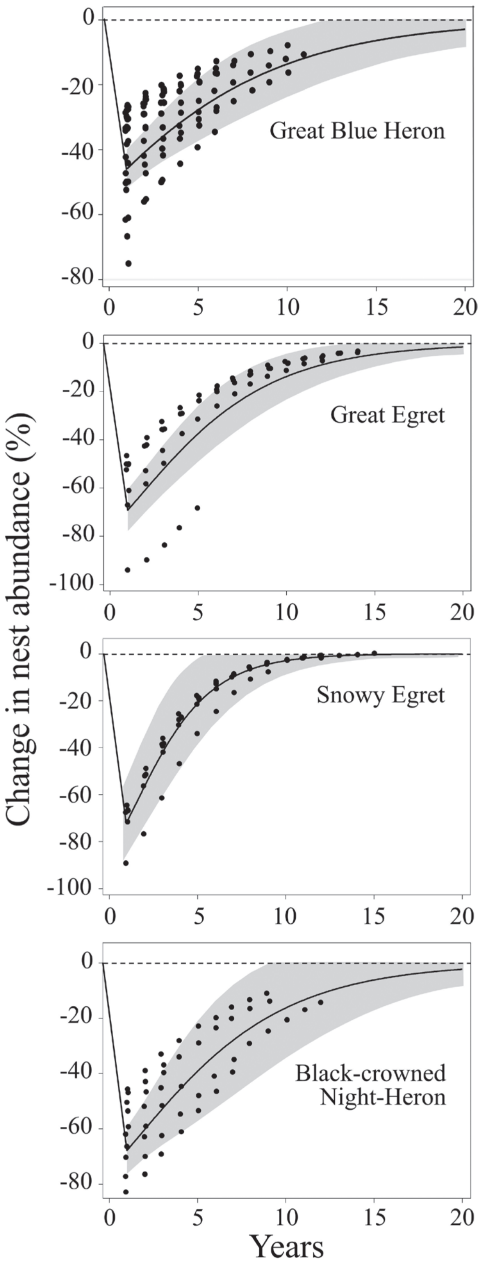

Figure 3. Predicted values of sudden major decline (Year 1) and associated recovery of annual $\log_e$ nest abundances of herons and egrets over 20 years within subregions of the northern San Francisco Bay Area, California, USA; values are generated by model parameters and back-transformed to represent percent annual change, relative to other underlying background dynamics and trends (controlled and reduced to zero; dashed line). Solid lines represent modeled patterns of impact and recovery after sudden major declines that drop below the lower 0.80 quantile of standard normal annual variation; shaded areas represent 95% confidence intervals; filled circles represent modeled predictions based on observed responses.

DISCUSSION

The recovery of ardeid nest abundances after a sudden major decline in a particular wetland area or subregion is likely to occur gradually over an extended number of years. Major subregional declines and extended periods of recovery can occur even when regional abundances are stable; in the San Francisco Bay Area, the nesting abundances of our study species are roughly stable or possibly increasing (Kelly *et al.* 2007; Kelly and Nur 2015). Our results further suggest that the annual rate of recovery is similar across thresholds used to define sudden major declines in nest abundance. At colony-site and subregional scales, average rates of annual nest success are generally high in years without major colony-site disturbance, but predation or other disturbance events reduce nest success and may prompt movements of individuals among colony sites or wetland subregions (Forbes *et al.* 1984; Pratt and Winkler 1985; Kelly *et al.* 2007). Therefore, the gradual rates of annual recovery we found may result from the recruitment of nesting adults or first-time breeders from surrounding subregions or other regions (Gibbs and Kinkel 1997).

Based on our results, annual recovery rates $(1-\hat{\delta})$, in the absence of other underlying trends or other processes affecting nest abundance, are similar among sudden major declines in subregional nest abundance that are more extreme than 80% of the annual variation. However, the expected impact on nest abundance *n* years after a particular sudden major decline in nest abundance ($\hat{\delta}^n \hat{\omega}$) depends strongly on the extent of initial impact , rather than on the rate of recovery. We cannot conclusively explain why, based on our results, Snowy Egret nest abundances apparently recover more quickly from sudden major subregional declines than other species (lower rates of impact persistence [$\hat{\delta}$]). Their faster recovery rates may be associated with their lower sensitivity, relative to other ardeids, to boat disturbance when foraging in estuaries (Bratton 1990), to direct nesting disturbance by humans (Parsons and Master 2000), and to a pattern of

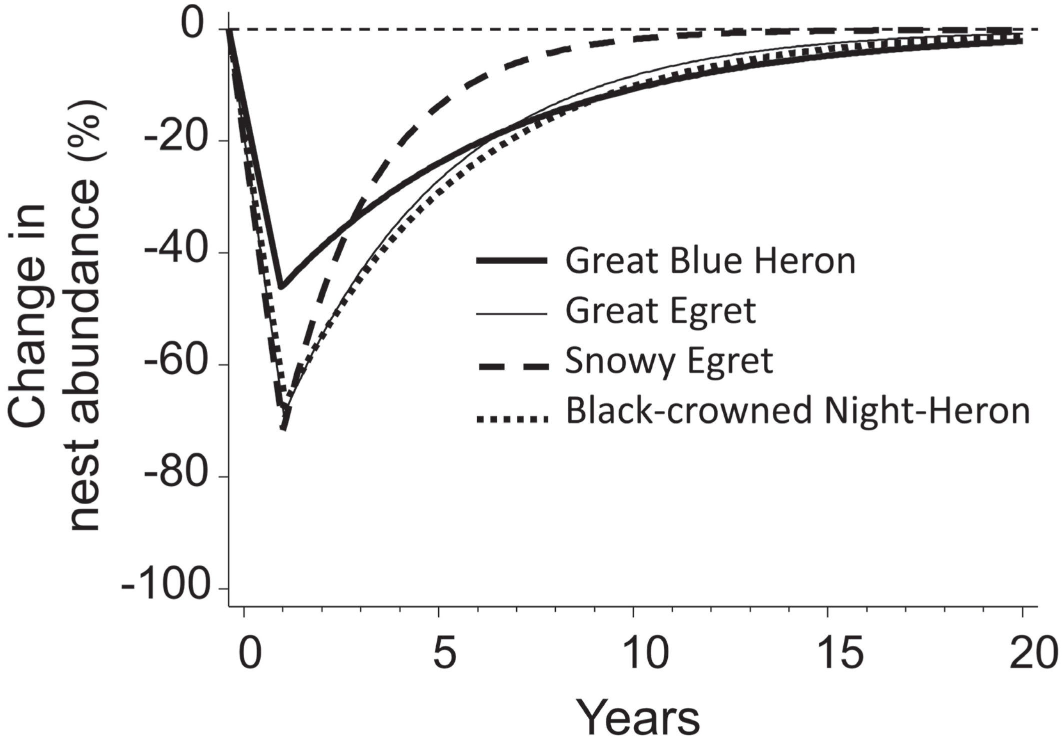

Figure 4. Percent change in subregional nest abundance of four ardeid species in years following sudden major declines in subregional nest abundance exceeding the lower 0.80 quantile of standard normal annual varialtion within 10 wetland subregions of the San Francisco Bay Area, California, USA, 1991-2010 (Table 4). The horizontal dashed line represents full recovery with a stable growth rate of zero, relative to other underlying trends.

colony-site selection near developed areas of the northern San Francisco Bay Area where they apparently tolerate higher levels of human activity (Kelly *et al.* 2007). In addition, the relatively fast recovery rates exhibited by Snowy Egrets may be related to their consistent use of mixed colony sites where other species may provide a continuing nesting stimulus (Burger 1981; Mashiko and Toquenaga 2014; Wyman *et al.* 2014). Further investigation is needed to evaluate the potentially confounding effects of other species on rates of recovery from sudden major declines in subregional nest abundance.

Great Blue Herons were subject to more frequent major declines in nest abundance than other species, but with relatively lower initial impact ($\hat{\omega}$). This is likely the outcome of establishing smaller, more widely distributed nesting colonies than our other study species (Kelly *et al.* 2007), possibly in response to higher rates of colony-site disturbance (Kenyon *et al.* 2007). The relatively slower subregional recovery rates we observed in Great Blue Herons are also consistent with potentially slower recruitment in less conspicuous, more isolated colony sites (Butler *et al.* 2000; Kelly *et al.* 2007). If Great Blue Herons establish multiple, smaller colonies in a given subregion, major disturbance at any particular colony site will result in a smaller impact on subregional nest abundance. Among our study species, the relatively lower initial impacts ($\hat{\omega}$) of sudden major subregional declines on Great Blue Heron nest numbers is reflected in relatively stable subregional and regional abundances over more than 25 years (Kelly *et al.* 2007; Kelly and Nur 2015).

Great Egrets experienced more severe sudden declines in subregional nest abundance than other species, particularly at the 0.95 threshold of major decline. Great Egrets nests are concentrated into fewer,

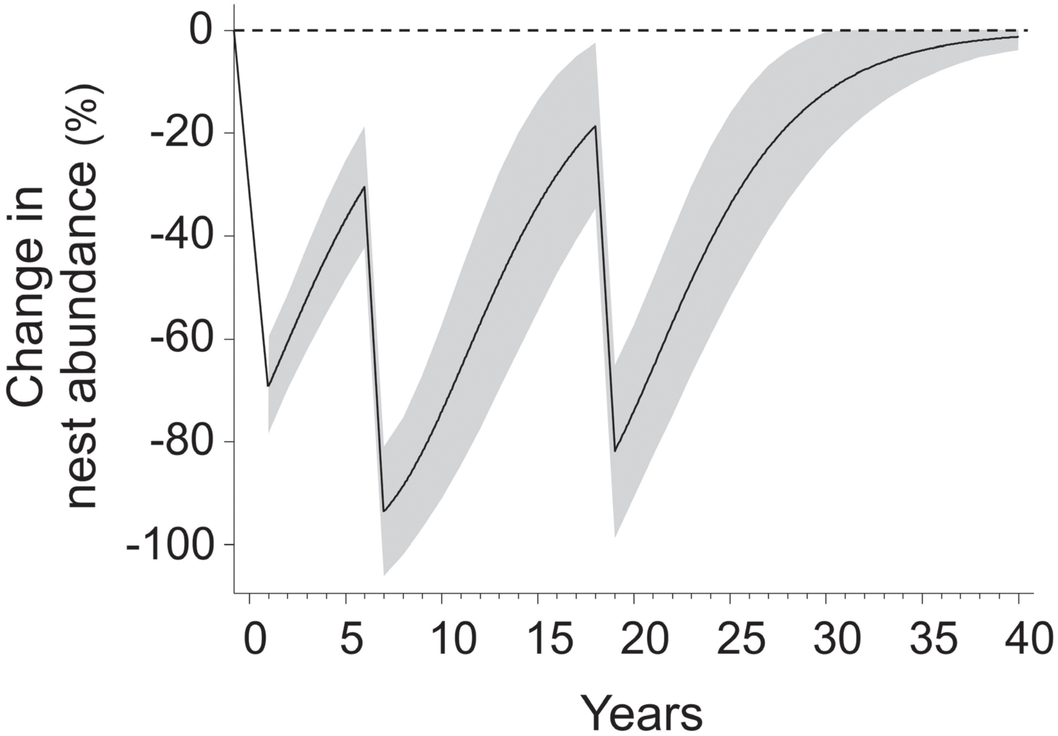

Figure 5. Predicted additive effects of repeated, major declines of -69%, -96%, and -86% in years 1, 7, and 19, respectively, on the recovery of subregional Great Egret nest abundance, based on an annual impact persistence of 0.79 (Table 4). The three major declines exceed, respectively, the lower 0.80, 0.95, and 0.90 quantiles of standard normal variation within 10 subregions of the San Francisco Bay Area, California, USA. The horizontal dashed line represents full recovery with a stable growth rate of zero, relative to other underlying trends.

larger colonies than Great Blue Heron nests (Kelly *et al.* 2007), and disturbance impacts on large colonies are likely to result in greater impacts on subregional nest numbers. Therefore, for Great Egrets and other species that tend to nest in large colonies, major disturbance at the colony-site level is likely to have greater impacts on subregional nesting abundance.

Underlying background dynamics and trends in annual nest abundance were controlled in our analysis, accounting for the expected (average) influences of background variation within and among subregions. Therefore, it is important to emphasize that the predicted recovery rates may be reduced or enhanced by variation in other processes operating at subregional, regional, or larger spatial scales. For example, subregional recruitment and recovery rates might increase if nesting dispersal from an adjacent subregion is temporarily enhanced by colony-site disturbance. Processes operating over larger spatial scales, including changes in population growth, nesting or natal dispersal, birth or death rates, or extrinsic processes such as weather or habitat change, might similarly reduce or enhance predicted subregional recovery rates after a sudden major decline in nest abundance (Butler 1994; Melvin *et al.* 1999; Fasola *et al.* 2010; Kelly *et al.* 2007). More obviously, predicted recovery from a sudden major decline in subregional abundance may be limited by concurrent degradation or loss of foraging habitat or by increased nesting disturbance by humans or potential nest predators.

The extended periods of recovery observed in our study suggest that the functional roles of ardeids as top wetland predators in particular subregional wetland systems might be affected for a substantial period of time after sudden major declines in nest abundance. As indicated by our results, the total time to recovery increases with the extent of initial impact. The magnitude of impacts during years with sudden major decline in nest abundance in the San Francisco Bay Area may differ from those in other areas. However, the similarity of recovery rates across levels of initial impact suggests that annual rates may primarily reflect species' inherent patterns of behavior or reproduction, such as low levels of colony-site fidelity (Simpson *et al.* 1987), spatial patterns of dispersal and intraregional movement (Melvin *et al.* 1999; Fasola *et al.* 2002), average (or maximum) levels of per capita productivity (Forbes *et al.* 1984; Rubolini and Fasola 2008), and foraging range (Smith 1995; Gibbs and Kinkel 1997; Kelly *et al.* 2008). If so, annual recovery rates at subregional scales might be similar among regions or vary over much larger geographic scales. Further investigation is needed to confirm whether ardeid numbers in subregions associated with more extensive wetland systems are more resilient to sudden major declines than those associated with smaller systems. Our estimated recovery rates offer a way to approximate the long-term impacts of major nesting disturbance, at one or more colony sites, on nest abundances at intermediate spatial scales related to the nesting and foraging needs of ardeids and the management of subregional wetland systems.

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