ABUNDANCE AND DISTRIBUTION OF THE COMMON RAVEN AND AMERICAN CROW IN THE SAN FRANCISCO BAY AREA, CALIFORNIA

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ABSTRACT: During the breeding season of 1999, we surveyed from roads in the San Francisco Bay area to determine the regional abundance and distribution of the Common Raven (*Corvus corax*) and American Crow (*C. brachyrhynchos*). Ravens concentrated along the outer coast and occurred in relatively low numbers in some interior areas, whereas the number of crows increased significantly from the outer coast to interior and bayshore locations. Both species occurred in significantly greater densities along urban and suburban survey routes than along rural routes, but dramatic exceptions were evident in some areas. Data from Breeding Bird Surveys, Christmas Bird Counts, and breeding bird atlases yielded similar distribution patterns. Breeding Bird Surveys and Christmas Bird Counts revealed strong regional increases in both species, but annual trends varied substantially at local scales. This variation, as well as significant abundance variation among survey routes, suggested considerable local differences in either habitat suitability or capacity for further population growth. Our results suggested that raven and crow populations may increase in both rural and developed areas undergoing rapid urbanization and that local conditions, rather than whether the habitat is rural or urban, may influence regional patterns.

Abundances of the Common Raven (*Corvus corax*) and American Crow (*C. brachyrhynchos*) have increased substantially over much of North America (Marzluff et al. 1994, Boarman and Heinrich 1999, Sauer et al. 2001). The Common Raven occurs throughout California but is scarce in much of the Central Valley, the central coast from the Santa Lucia Mountains south to northwestern Ventura County, and irrigated portions of the Coachella, Imperial and lower Colorado River valleys in the southeast corner of the state. The American Crow is widespread but absent from some drier western parts of the San Joaquin Valley, interior foothills, and the southeastern deserts (Small 1994). Throughout their range, ravens appear to be invading agricultural areas to a greater extent than urban areas (but are common in many urban areas), whereas crows appear to be invading urbanized areas more rapidly than agricultural areas (Marzluff et al. 1994, Marzluff and Restani 1999). Both species are resident through most of the San Francisco Bay area, a highly urbanized region with large sections that remain undeveloped or used for agriculture. Both species have increased in number recently in the southern portion of the region (Coston 1998). The overall status and distribution of these corvids within the San Francisco Bay area, however, have not been addressed.

To determine the abundance and distribution of ravens and crows in the San Francisco Bay area, we surveyed the region during the spring of 1999 (Figure 1). Because field observations were limited to repeated road surveys along particular routes within a single season, we compared the results with existing Breeding Bird Survey (BBS; Sauer et al. 2001), Audubon Christmas

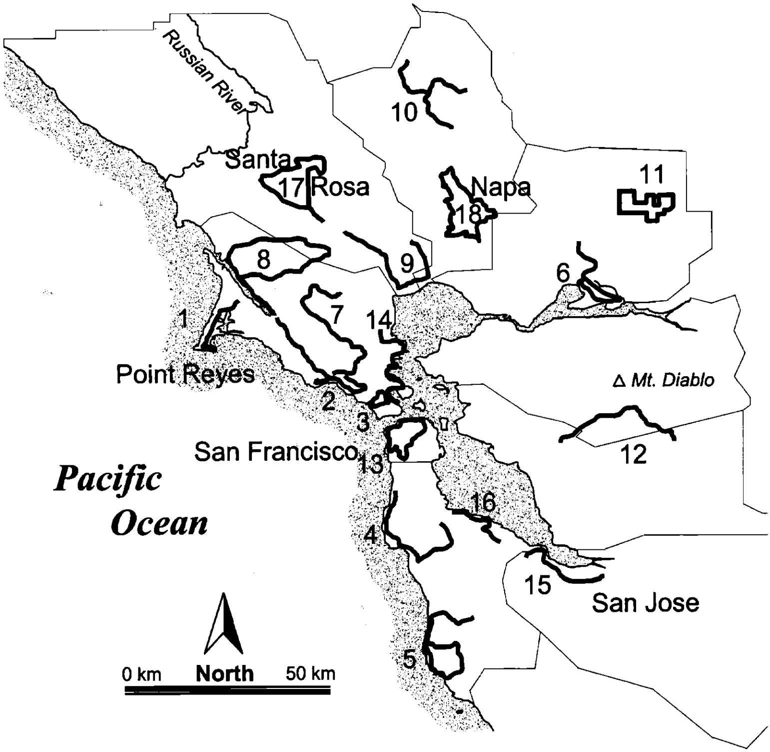

Figure 1. Routes used in road surveys of Common Ravens and American Crows in the San Francisco Bay area. Labels, route-identification numbers; thin lines, county boundaries (see Figures 5 and 6 for county names).

Bird Count (CBC; Butcher 1990), and breeding bird atlas (BBA; Robbins 1990) data to provide a more thorough perspective on regional distribution and to evaluate local and regional trends in abundance of these species.

STUDY AREA

The study area covered all nine counties adjacent to San Francisco Bay: Marin, Sonoma, Napa, Solano, Contra Costa, Alameda, Santa Clara, San Mateo, and San Francisco (Figure 1). The study area did not extend into the delta east of the confluence of the Sacramento and San Joaquin rivers. We did not conduct road surveys along the outer coast of Sonoma County or along the East Bay shoreline, although these areas are included in analyses of BBS, CBC, and BBA data. Analysis of BBS data included some routes that extended slightly beyond the bay area counties, into coastal Santa Cruz County to the south, coastal Mendocino County to the north, San Joaquin County to the east, and Yolo County to the north (Figure 2).

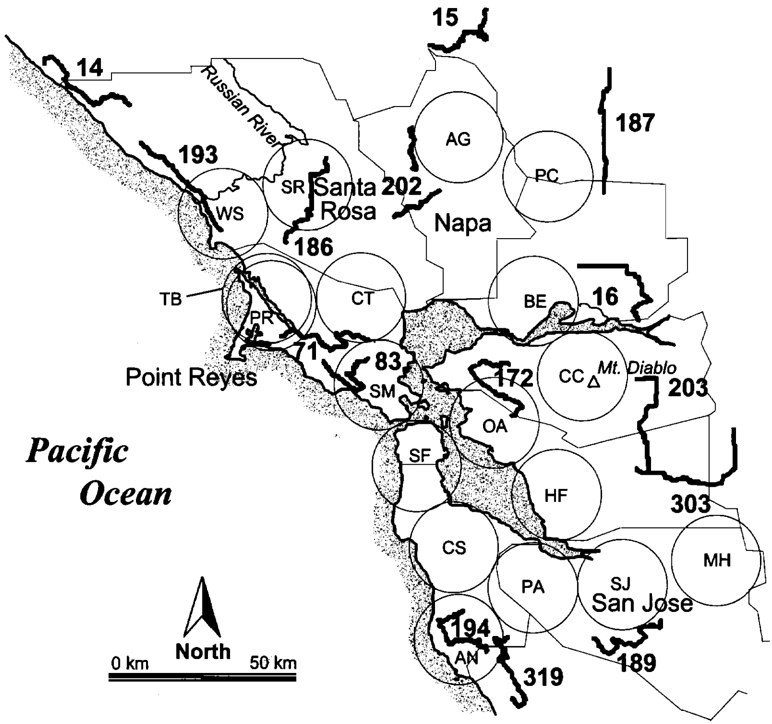

Figure 2. Breeding Bird Survey routes (bold lines and associated number codes) and Christmas Bird Count circles (letter codes) in the San Francisco Bay area. Thin lines, county boundaries (see Figures 5 and 6 for county names). See Tables 2, 3, and 4 for details on each route or circle.

Above the coastal terraces and alluvial shorelines, the area is characterized by rolling hills and mountains of the Coast Range. Moist coast redwood (*Sequoia sempervirens*), Douglas fir (*Pseudotsuga menziesii*), and mixed broad-leaved evergreen forests dominate the outer coastal drainages, giving way to wider expanses of grassland, chaparral, and oak woodland to the east. Nonnative eucalyptus (predominantly blue gum, *Eucalyptus globulus*) occurs throughout the region in patches mostly smaller than one hectare or as narrow windbreaks.

Urban and suburban habitats are concentrated in central Sonoma County near Santa Rosa, in southern Napa County near Napa, and south of Sonoma, Napa and Solano counties along bay shorelines. The shoreline and terraces along the outer coast and northern San Pablo and Suisun bays are generally rural and open. Rural areas are primarily used for agriculture, with range cattle production dominating most areas, dairy ranching locally dominant in the Point Reyes area, and farms and vineyards characterizing much of the northern portion of the region.

METHODS

From 26 March through 21 June 1999 we counted Common Ravens and American Crows along 18 survey routes averaging 49 ± 14.0 (standard deviation) km in length, established along roads throughout the region (Figure 1). We recruited 40 experienced birders, capable of distinguishing crows and ravens in the field, as volunteer observers to conduct mid-morning road surveys along each route twice monthly on standardized dates. Because each observer consistently surveyed the same route, rather than rotating among routes, observer variability could have influenced the results to an unknown extent. Survey teams consisting of one driver and one observer traveled at speeds of 56 to 72 km/h. Each survey began from a standard starting point. For each raven or crow observation, observers recorded the distance along the survey route, species name, group size (number of individuals within 100 m of each other), and perpendicular distance (<100 m, 100–200 m, or >200 m) from the road.

We distributed survey routes systematically to sample two land-use types (>75% rural vs. >75% urban/suburban) and three subregions (outer coast, bay shore, and inland). We apportioned the routes to approximate the extent of each land-use type and subregion within the study area and maximized the distances between routes to ensure independence of counts (Figure 1). To keep survey speed down, we avoided freeways and major highways. In urbanized areas, we selected routes that allowed observers to maintain normal survey speeds, although temporary slowing was necessary on some occasions. Given these constraints, suitable survey routes for each land-use type and subregion were sometimes determined by available roads. Open/rural habitat in the interior of the eastern portion of the study area and salt ponds in the southern part of the bay were undersampled relative to their extents.

We used the number of birds observed per kilometer of survey route to index corvid densities. We then examined differences between rural and urban/suburban habitats, and among coastal, interior, and bayshore locations using analysis of variance. Before analysis, we (natural) log-transformed the data so that densities did not differ significantly from normality ($P <$ 0.05). Post hoc tests for differences among groups included Bonferroni adjustments for experimentwise error. Because routes were selected systematically on the basis of land use, subregion, and availability of roads, we modeled variation among routes nested within land use and location types as fixed effects. However, because routes covered a substantial portion of the study area and were selected to achieve a representative sample of regional populations, we also tested (wherever indicated in Results) the effects of land use and subregion against "random" variation among routes as a proxy for other, unknown influences on general regional patterns (Bennington and Thayne 1994). Indications of such influences should be interpreted cautiously because selection of survey routes was systematic rather than random.

We also examined BBS and CBC data, to determine regional trends in the numbers of ravens and crows and to compare abundances with patterns suggested by our road-survey data. The BBS is also a roadside survey, based on 50 three-minute point counts conducted along thousands of 39.4-km routes over much of North America (Sauer et al. 2001). Because BBS surveys date back as far as 1966, they provide a perspective on changes in regional breeding-season abundance. We examined long-term trends in winter abundance with CBC data, which are based on total counts conducted annually within standard circles of 24.1-km diameter (458 km^2; Butcher 1990). We analyzed BBS and CBC trends by linear route regression, with regional trends expressed in percent change per year weighted by mean abundance and number of years covered at each BBS route or CBC location (Butcher et al. 1990, Geissler and Sauer 1990). We estimated the mean and variance of regional trends from 400 random bootstrap subsamples drawn with replacement from the original sample of trends (Geissler and Sauer 1990, Thomas and Martin 1996). CBC counts were standardized to reflect expected abundances and trends for the average effort (175 party-hours) in the study area over all count circles and years, using the procedure described by Butcher and McCulloch (1990; survey effort had no significant effect on raven numbers, $P > 0.90$). We modified calculation of the exponent relating survey effort to number of birds counted by including terms in the model (dummy variables) to account for unbalanced effects of CBC locations on the overall relation between effort and abundance. We did not adjust further for differences in effort, which include annual differences in distance covered per party-hour and distribution of effort among habitat types of varying suitability (e.g., ranch land vs. open water), although we considered habitat differences among count circles when interpreting the results. We emphasize that trends and abundances based on CBC data should be evaluated with considerable caution and confirmed by additional study because of these and other potential sources of error, including problems with identification, counting, weather, access, and habitat coverage (Butcher 1990).

We further evaluated regional breeding distributions by compiling breeding bird atlas (BBA) data within the study area. BBAs use standardized criteria to determine the breeding status (possible, probable, confirmed) of each bird species within 5-km^2 blocks (Robbins 1990) and are organized and developed separately by county (Marin County: Shuford 1993; Sonoma County: Burridge 1995; Napa County: R. Leong and B. Grummer, unpubl.; Contra Costa County: S. Glover, unpubl.; Alameda County: B. Richmond and H. Cogswell, unpubl.; Santa Clara County: Santa Clara Atlas Comm., unpubl.; San Mateo County: R. Johnson, unpubl.; San Francisco County: M. Eaton, unpubl.). Where atlas blocks spanned BBA (county) boundaries, we used the status code from the BBA that indicated the greatest likelihood of breeding for that location.

RESULTS

Differences in corvid numbers among survey routes, nested within land-use type or subregion, were greater than expected by the variability within routes ($F = 40.65$; df = 10, 110; $P < 0.0001$), indicating that variation among survey routes accounted for significant regional variability in corvid densities (Table 1, Figure 1). On average, 89% ± 2.3 (standard error) of ravens and 92% ± 1.8 of crows were observed within 200 m of survey

Table 1 Number of Common Ravens and American Crows Observed During Road Surveys in the San Francisco Bay Area During the Breeding Season of 1999

					Birds per kilometer			
					Common Raven		American Crow	
Route	Land Use	Subregion	Length (km)	*N*	Mean	(SE)[a]	Mean	(SE)
1	Rural	Coast	19.4	12	0.584	(0.290)	0.014	(0.010)
2	Rural	Coast	59.4	18	0.040	(0.005)	0.222	(0.030)
3	Rural	Coast	33.0	7	0.241	(0.081)	0.322	(0.078)
4	Rural	Coast	41.6	7	0.169	(0.024)	0.034	(0.014)
5	Rural	Coast	50.8	7	0.128	(0.018)	0.000	(0.000)
6	Rural	Bay	41.0	7	0.038	(0.019)	0.056	(0.025)
7	Rural	Interior	50.7	2	0.089	(0.010)	0.335	(0.177)
8	Rural	Interior	79.8	6	0.029	(0.013)	0.090	(0.023)
9	Rural	Interior	65.2	6	0.070	(0.036)	0.116	(0.039)
10	Rural	Interior	40.9	4	0.006	(0.006)	0.000	(0.000)
11	Rural	Interior	51.0	8	0.007	(0.005)	2.457	(0.567)
12	Rural	Interior	41.8	3	0.016	(0.016)	0.318	(0.076)
13	Urban/Suburban	Coast	39.6	7	0.375	(0.086)	0.007	(0.005)
14	Urban/Suburban	Bay	46.2	7	0.012	(0.009)	0.444	(0.079)
15	Urban/Suburban	Bay	50.4	6	0.205	(0.016)	0.251	(0.054)
16	Urban/Suburban	Bay	41.8	6	0.134	(0.040)	0.017	(0.017)
17	Urban/Suburban	Interior	63.1	7	0.238	(0.036)	0.253	(0.044)
18	Urban/Suburban	Interior	65.4	5	0.003	(0.003)	0.281	(0.075)

[a]SE, standard error.

routes, with 69% ± 4.4 of ravens and 70% ± 7.1 of crows observed within 100 m. The proportion of crows or ravens that occurred in pairs, suggesting possible breeding status, did not differ significantly by land use, subregion, or route ($P > 0.05$).

American Crow

In general, densities of American Crows along rural and urban/suburban survey routes did not differ significantly ($F = 1.76$; df = 1,110; $P = 0.19$). If route 11, an open agricultural area with unusually high numbers of crows (Table 1) was excluded, however, crows were significantly more abundant along urban/suburban survey routes than along the remaining rural routes ($F = 10.9$; df= 1, 103; $P < 0.01$; Figure 3). When tested against random route effects (see Methods), the number of crows in rural and urban/suburban areas did not differ significantly ($F = 0.39$; df = 1, 15; $P = 0.54$).

Densities of crows along survey routes did vary significantly by subregion ($F = 50.5$; df = 2, 110; $P < 0.0001$), with numbers increasing significantly from the outer coast to the bay shore to the interior ($P < 0.01$). If route 11, an interior route with unusually high numbers of crows (Table 1) was excluded, densities in bayshore and interior locations did not differ ($P >$

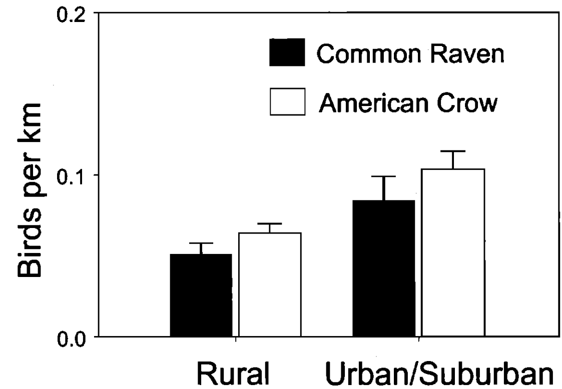

Figure 3. Mean number of Common Ravens and American Crows observed per kilometer of survey route by rural or urban/suburban land use in the San Francisco Bay area. Values for the American Crow exclude route 11 (see text). Error bars, standard errors.

0.99; Figure 4). Despite significantly lower densities of crows along outer-coast routes, differences by location were not significantly greater than the estimated random variation across the region (random effects $F = 1.54$; df=2, 15; $P = 0.25$). Land use and subregion influenced the number of crows on each route independently ($F = 0.13$; df = 2, 112; $P > 0.87$).

Common Raven

Densities of Common Ravens were significantly greater along survey routes in urban/suburban than in rural areas ($F = 5.75$; df = 1, 107; $P = 0.02$; Figure 3). In contrast, the highest numbers of ravens occurred in the pastoral zone of Point Reyes National Seashore (route 1; Table 1, Figure 1). Land-use effects did not differ significantly from estimated random variation in the region (random route effects $F = 0.70$; df = 1, 16; $P = 0.41$).

Raven densities varied significantly by subregion ($F = 18.66$; df = 2, 107; $P < 0.0001$), with numbers increasing significantly from interior to bayshore to outer-coast survey locations ($P < 0.05$; Figure 4). The test for random route effects revealed a significant contrast between the outer-coast routes and the bay shore or interior ($F = 5.12$; df = 1, 15; $P = 0.04$). Therefore, higher concentrations of ravens characterize the outer coast. Land use and subregion influenced the number of ravens on each route independently ($F = 0.003$; df = 2, 108; $P > 0.95$).

Other Survey Data

Numbers of ravens and crows observed along 15 BBS routes in the San Francisco Bay area reveal distribution patterns similar to those suggested by our road survey, including dramatic abundance variation from route to route (Table 2). BBS data suggest significant overall annual increases in both ravens (5.16% ± 0.15; $P < 0.001$) and crows (3.21% ± 0.13; $P < 0.001$).

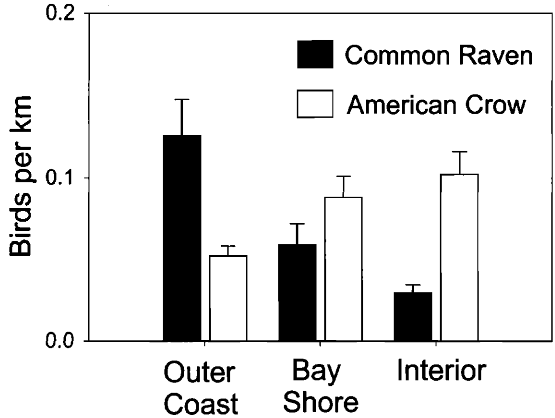

Figure 4. Mean number of Common Ravens and American Crows observed per kilometer of survey route in outer coast, San Francisco Bay shore, and interior subregions in the San Francisco Bay area. Values for the American Crow exclude route 11 (see text). Error bars, standard errors.

BBS trends vary greatly across the region, however, suggesting effects at smaller scales (Table 2). BBS data imply strong increases in the number of ravens along the southern outer coast of the study area and in central Napa County. They suggest significant increases in crows near Santa Rosa and along part of the outer Sonoma coast. Crows apparently increased along route 203 in the eastern interior of Contra Costa and Alameda counties from 1972 to 1991 but declined along nearby BBS route 303 from 1992 to 1999 (Table 2, Figure 2). Inspection of scatterplots for all individual routes, however, suggested that such differences may depend on the number of years surveyed, because linear slopes measured over periods of less than 8–10 years may contrast with longer-term trends.

CBC data reveal significant overall annual increases since 1950 in numbers of both ravens (6.57% ± 0.12; $P < 0.001$) and crows (3.31% ± 0.05; $P < 0.001$), increases that accelerated during the 1980s and 1990s (ravens: 7.23% ± 0.16, $P < 0.001$; crows: 5.02% ± 0.08, $P < 0.001$). Patterns of variation in abundance by CBC circle are generally consistent with road-survey and BBS results and suggest substantial local variation in numbers of both ravens and crows (Tables 3 and 4).

In neither BBS or CBC results did we find significant correlations, positive or negative, between the two species' abundances or trends ($P < 0.05$), suggesting their distributions are independent. In contrast, our road surveys imply a significant inverse relationship between raven and crow abundances ($r = -0.55$, $P < 0.05$), suggesting their distributions are complementary. For example, raven and crow numbers varied dramatically among urbanized routes, with high numbers of ravens in San Francisco but relatively few crows, and surprisingly low numbers of ravens along the urbanized corridor

Table 2 Breeding Bird Survey Trends and Mean Number of Birds per Survey Route for the Common Raven and American Crow in the San Francisco Bay Area

			American Crow		Common Raven	
BBS route[a]	Period	Years surveyed	Trend (% per year)[b]	Mean birds per route	Trend (% per year)[b]	Mean birds per route
14	1968–2000	31	-3.27	0.55	2.33**	20.48
15	1969–2000	27	-11.12	2.52	10.00	1.81
16	1968–2000	18	6.80	6.39	19.92	1.17
71	1971–2000	24	1.82	20.75	6.45	7.83
83	1975–2000	25	1.34	17.18	0.36	7.65
172	1972–2000	19	-10.92	4.05	0.00	0.05
186	1972–2000	28	9.07**	52.50	0.32	1.86
187	1972–1988	14	12.30**	24.78	0.00	0.21
189	1972–2000	20	3.04	25.30	9.42	0.45
193	1972–2000	25	19.89*	1.12	-5.40**	8.88
194	1972–1995	23	-1.40	0.07	18.10*	0.52
202	1972–1997	26	0.12	29.54	10.93**	4.81
203	1972–1991	20	13.07**	13.30	-6.83	0.15
303	1992–1999	7	-8.13**	124.43	6.75	6.43
319	1992–1996	5	0.00	0.00	37.02*	18.20

[a]See Figure 2 for location.
[b]Linear trend significant at $^{*}P < 0.05$, $^{**}P < 0.01$.

of eastern Marin County where crows were relatively abundant (routes 13 and 14, Table 1).

Composite breeding bird atlases for the region reflect distributions that are generally consistent with the road surveys and BBS (Figures 5 and 6). We emphasize that atlas data for the bay area represent a wide range of sampling periods dating back as far as the late 1970s and should therefore be interpreted with considerable caution and careful comparisons with other available data. BBAs indicate Common Raven concentrations along the outer coast, particularly in the Point Reyes area and along the San Francisco and San Mateo coast, in urbanized areas along the southern San Francisco Bay shoreline, in some higher elevations of eastern Contra Costa, Alameda, and Santa Clara counties, and in parts of Napa county. Such "concentrations" are based on a greater frequency of 5-km^2 blocks with breeding ravens, rather than greater raven abundances per se. However, broad areas with breeding confirmed over many adjacent blocks are likely to support more ravens than areas where breeding is confirmed in only a few blocks. Breeding ravens appear to be relatively scarce in large areas of central Contra Costa, Alameda, and Santa Clara counties and in relatively low numbers in central Sonoma County. BBAs reveal that the American Crow's breeding distribution is relatively continuous in most bayshore and interior areas (although habitat is not necessarily saturated) but sparse or broken in many parts of the outer coastal drainage (Figure 6). In addition to resembling

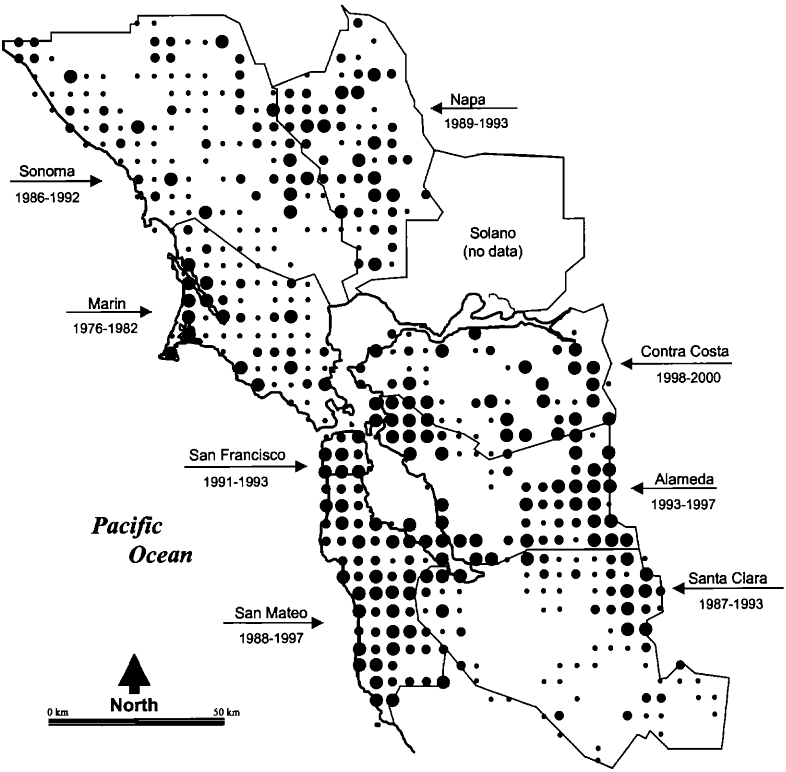

Figure 5. Breeding distribution of the Common Raven in the San Francisco Bay area, based on breeding bird atlas data. Filled circles indicate likelihood of breeding in each 5-km block: large circle, confirmed; medium circle, probable; small circle, possible; no circle, no ravens observed. Field data were collected in the years indicated under each county name.

patterns emerging from the road survey and BBS (Tables 1 and 2), BBA patterns are generally consistent with winter distributions indicated by CBC results. CBCs, however, suggest lower concentrations of ravens along the east side of southern San Francisco Bay and higher concentrations of crows in western Sonoma County (Tables 3 and 4).

DISCUSSION

Increases in the numbers of ravens and crows in the San Francisco Bay area are consistent with increases throughout the western United States, but in the bay area raven distribution differs from patterns evident at larger scales with regard to urbanization (Marzluff et al. 1994). BBS data imply that Common Raven densities in the western United States are negatively

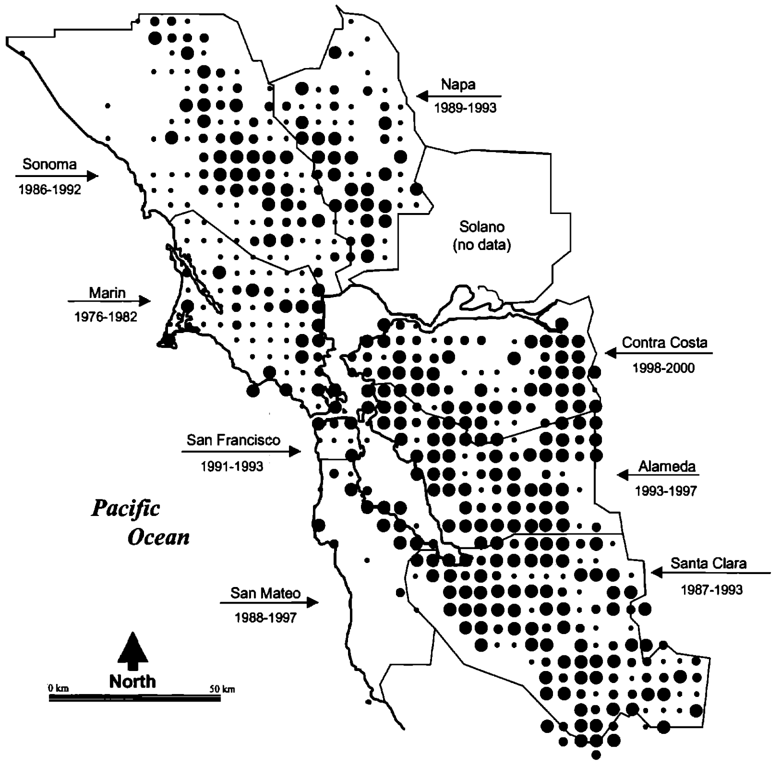

Figure 6. Breeding distribution of the American Crow in the San Francisco Bay area, based on breeding bird atlas data. Filled circles indicate likelihood of breeding in each 5-km block: large circle, confirmed; medium circle, probable; small circle, possible; no circle, no ravens observed. Field data were collected in the years indicated under each county name.

associated with human densities (although less strongly in coastal states), with ravens apparently invading agricultural areas to a greater extent than urban areas (Marzluff et al. 1994). In contrast, we found greater raven densities along urbanized survey routes, on average, than along rural survey routes, a pattern similar to that in the Mojave Desert (Knight et al. 1993). However, both our highest and lowest raven densities were along rural routes, the highest in the agricultural zone of Point Reyes National Seashore (dominated by dairy ranches), and the lowest in the rural interior of Alameda and Napa counties.

Common Ravens occurred in significantly greater densities along the outer coast than in the interior of the region or near the bay (although the east bay shoreline was not included in our road survey). In such coastal habitats, ravens feed on livestock carcasses, grain in cattle feedlots, and a

Table 3 Christmas Bird Count Trends and Mean Number of Birds per Count Circle for the American Crow in the San Francisco Bay Area

	1950–1998			1980–1998		
Count Circle[a]	Years	Trend (% per year)[b]	Mean birds per circle	Years	Trend (% per year)[b]	Mean birds per circle
Angwin (AG)	39	3.66***	516.10	18	−0.69	681.75
Año Nuevo (AN)	26	3.01	2.50	18	−3.34	3.36
Arroyo Cheap Thrills (CT)	10	2.96	1543.27	8	1.65	1604.26
Benicia (BE)	37	17.77***	50.86	19	15.24***	96.46
Contra Costa (CC)	43	9.06***	46.90	19	8.73**	69.46
Crystal Springs Reservoir (CS)	41	6.33***	16.36	18	23.92***	32.99
Hayward–Fremont (HF)	29	1.45	72.99	17	10.90***	62.85
Mount Hamilton (MH)	21	1.24	101.75	19	4.25	97.27
Oakland (OA)	45	4.01***	43.96	18	5.31*	56.73
Palo Alto (PA)	39	14.81***	22.86	19	13.24***	43.39
Point Reyes (PR)	27	1.56*	605.44	19	−0.15	653.41
Putah Creek (PC)	26	10.52***	316.29	19	16.28***	382.64
San Francisco (SF)	29	10.51***	36.97	15	23.48***	70.28
San Jose (SJ)	47	0.18	180.47	19	9.61***	148.48
Santa Rosa (SR)	36	0.49	1547.83	19	4.70***	1581.53
Southern Marin County (SM)	23	7.56***	494.32	19	6.39***	556.13
Tomales Bay (TB)	13	2.63	365.71	0		
Western Sonoma County (WS)	31	4.03***	241.11	19	2.19	284.10

[a]See Figure 2 for location.

[b]Linear trend significant at $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

variety of other foods found in grasslands, at public picnic areas, and along dunes and beaches (Roth et al. 1999). Ravens also exploit garbage dumps (Marzluff et al. 1998), which are often located in rural areas. However, our road survey indicated that high raven numbers in coastal agricultural areas are matched by similarly high numbers in the most urbanized habitats around San Francisco Bay.

Although our road survey did not include urban areas in the east bay, BBA data show that breeding ravens and crows are established there, and CBC data suggest significant increases in both species. Over the past 20 years, ravens have established themselves and increased their numbers near salt ponds along the southern east bay shoreline (H. Cogswell pers. comm.).

The number of American Crows in California increased dramatically with the spread of agriculture in the early 1900s (Emlen 1940). BBS data, however, show that crow abundances in the western United States are negatively associated with the extent of farmland and positively correlated with human population density (Marzluff et al. 1994). Consistent with this pattern, our results revealed that crows concentrate in urbanized habitats

Table 4 Christmas Bird Count Trends and Mean Number of Birds per Count Circle for the Common Raven in the San Francisco Bay Area

	1950–1998			1980–1998		
Count Circle[a]	Years	Trend (% per year)[b]	Mean birds per circle	Years	Trend (% per year)[b]	Mean birds per circle
Angwin (AG)	40	9.18***	23.53	19	5.53*	35.84
Año Nuevo (AN)	26	19.39***	30.62	18	14.57***	43.50
Arroyo Cheap Thrills (CT)	10	-1.00	60.40	8	0.84	57.75
Benicia (BE)	37	8.02***	4.65	19	9.72**	8.32
Contra Costa (CC)	43	5.70***	2.14	19	7.47**	4.21
Crystal Springs Reservoir (CS)	42	12.86***	27.95	18	25.16***	62.22
Hayward–Fremont (HF)	30	3.93*	2.07	18	12.87**	2.89
Mount Hamilton (MH)	21	9.13***	24.57	19	9.21***	26.32
Oakland (OA)	46	8.99***	8.59	18	17.86***	21.17
Palo Alto (PA)	39	15.66***	23.95	19	12.09***	47.95
Point Reyes (PR)	28	0.87	347.57	19	0.58	365.32
Putah Creek (PC)	27	11.76***	9.89	19	18.13***	13.37
San Francisco (SF)	29	7.21***	40.69	15	18.32***	73.07
San Jose (SJ)	47	5.69***	7.09	19	25.07***	14.11
Santa Rosa (SR)	35	5.18***	22.06	19	6.73***	28.00
Southern Marin County (SM)	23	8.29***	125.87	19	8.98***	140.63
Tomales Bay (TB)	13	22.39***	170.31	0		
Western Sonoma County (WS)	28	2.17**	208.75	16	-0.75	230.38

[a]See Figure 2 for location.

[b]Linear trend significant at $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

over most of the San Francisco Bay area and occur in relatively low numbers in many rural areas. Yet there is a dramatic exception to this pattern in farmland northeast of Suisun Bay (Route 11), where we found the highest regional densities of crows; the reasons for these high densities are unknown.

Breeding ravens and crows generally move less than 3–7 km per day (Engel and Young 1992, Linz et al. 1992, Sullivan and Dinsmore 1992, Caccamise et al. 1997, Roth et al. 1999). Therefore, the 50-km routes used in our road survey were probably of a length suitable to capture differences in local abundance near the appropriate scale of landscape use. Although we did not measure detection probabilities associated with distance from the road, ravens and crows are relatively conspicuous birds; their dramatically higher densities within 100 m of survey roads suggest habits of foraging on highway-generated carrion (Knight and Kawashima 1993).

The effects of landscape properties on population growth cannot be determined from our count data because differences in bird density might not be related to productivity or survivorship. Studies based on individually marked birds are needed to determine if behavioral adjustments to urbanization or anthropogenic food sources lead to changes in crow or raven population growth or distribution (Knight et al. 1987, Marzluff et al. 1998). Of particular concern is whether increases in numbers of ravens and crows might signal increases in nest predation of other native species, including waterfowl (Stiehl and Trautwein 1991), the Marbled Murrelet (*Brachyramphus marmoratus*; Singer et al. 1991, Nelson and Hammer 1995), Snowy Plover (*Charadrius alexandrinus*; U. S. Fish and Wildlife Service 1993), Least Tern (*Sterna antillarum*; Fancher 1992, Avery 1995), Common Murre (*Uria aalge*; Thayer et al. 1999, Roth et al. 1999), herons and egrets (Ardeidae; Parsons 1995, Kelly and Fischer 2000), and forest-nesting passerines (Andren 1992, Buler and Hamilton 2000). However, corvid numbers may correlate poorly with overall nest-predation rates, especially if changes in corvid abundance influence rates of nest predation by other species (Clark et al. 1995). Additional studies are needed to test for the independent effects of increasing corvid densities on the population dynamics of other species.

With the exception of a greater concentration of ravens along the outer coast, variation in abundance of crows and ravens among coastal, bayshore, and interior subregions did not seem to exceed random differences in the region. Similarly, variation in corvid numbers and trends suggests substantial variation with local conditions. Also, the inverse relationship between abundances of ravens and crows did not correspond to differences in rural vs. urbanized habitat and was not significant in other available data. Thus, factors affecting differences in species distribution and habitat use may be complex, with local-scale habitat variation influencing the general regional pattern. Further study is needed to determine the extent to which local conditions reflect differences in habitat suitability for foraging or breeding, or alternatively, differences in habitat saturation and associated capacity for further population growth.

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