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CALIFORNIA BLACK RAILS IN THE SAN FRANCISCO BAY REGION: SPATIAL AND TEMPORAL VARIATION IN DISTRIBUTION AND ABUNDANCE¹

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Abstract. We conducted surveys at 352 listening stations in 26 tidal marshes in the San Francisco Bay region in 1996 that we had surveyed previously in 1986-1988. The majority of these marshes were associated with San Pablo Bay ($n = 14$ marshes, 53.9%); the remainder were associated with Suisun Bay and Carquinez Strait ($n = 5$, 19.2%) or the outer coast ($n = 7$, 26.9%). Estimates of density for California Black Rails are confounded by a variety of environmental factors, as well as movement of birds in response to the playback of tape recordings of vocalizations. We attempted to control inherent bias, interpolated abundance indices from our data, and derived abundance rankings for discrete representative marshes associated with San Francisco Bay and the outer coast. Compared to 1986-1988, slightly higher detection rates were encountered in San Pablo and Suisun bays during 1996, but lower rates were encountered on the outer coast. An analysis of interdecadal variation suggested an increase in the populations in San Pablo and Suisun bays and a decrease in the isolated populations in the outer coast marshes, however those trends did not cross the threshold of significance. We found that the probability that rails were present in a marsh increased significantly as marsh size increased. We also analyze the relationship between marsh size and abundance indices, and discuss factors that bias estimates as well as summarize factors that likely influence the population distribution of rails.

Keywords: abundance index, Black Rail, California, *coturniculus*, abundance indices, DISTANCE, San Francisco Bay, tidal marshland, *Laterallus, jamaicensis*.

LA POLLUELA NEGRA DE CALIFORNIA EN LA REGIÓN DE LA BAHÍA DE SAN FRANCISCO: VARIACIÓN ESPACIAL Y TEMPORAL EN DISTRIBUCIÓN Y ABUNDANCIA.

Resumen. Muestreamos 352 estaciones de escucha en 26 humedales de marea de la región de la Bahía de San Francisco en 1996, previamente muestreadas de 1986 a 1988. La mayoría

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de los humedales están asociados a la Bahía de San Pablo ($n = 14$ humedales, 53.9%); el resto están asociados con la Bahía Suisun y el Estrecho de Carquinez ($n = 5$, 19.2%) o la costa del Pacífico ($n = 7$, 26.9%). Las estimas de densidad de la polluela negra de California (*Laterallus jamaicensis coturniculus*) contienen sesgos causados por diversos factores ambientales, así como por el movimiento de las aves como consecuencia del play-back de grabaciones de vocalizaciones. Intentamos controlar el sesgo intrínseco, realizamos interpolaciones de índices de abundancia a partir de nuestros datos, y derivamos rankings de abundancia para humedales representativos asociados con la Bahía de San Francisco y la costa del Pacífico. Comparado con el periodo 1986-1988, en 1996 encontramos tasas de detección ligeramente más altas en las bahías de San Pablo y Suisun, pero las tasas fueron más bajas en la costa. Los análisis de variación interdecadal sugieren aumentos en las poblaciones de las bahías de San Pablo y Suisun, y un declive en las poblaciones aisladas de la costa, aunque estas tendencias no son significativas. Encontramos que la probabilidad de que las polluelas estén presentes en un humedal aumenta significativamente con el tamaño del mismo. También analizamos la relación entre el tamaño del humedal y los índices de abundancia, discutimos los factores que pueden sesgar las estimas y resumimos los factores que probablemente influyen en la distribución de las polluelas.

Palabras clave: índice de abundancia, polluela negra, California, *Laterallus jamaicensis coturniculus*, DISTANCE, Bahía de San Francisco, humedal de marea.

LES RALES NOIRS DE CALIFORNIE DANS LA REGION DE LA BAIE DE SAN FRANCISCO: VARIATION SPATIALE ET TEMPORELLE DE DISTRIBUTION ET D'ABONDANCE

Résumé. En 1996, nous avons réalisé des recensements sur 352 stations d'écoute dans 26 marécages de marée de la région de la Baie de San Francisco que nous avons déjà recensés en 1986-1988. La majorité de ces marécages étaient associés à la Baie de San Pablo ($n = 14$ marécages, 53.9%), les autres à la Baie de Suisun et au Détroit de Carquinez ($n = 5$, 19.2%) ou à la côte extérieure ($n = 7$, 26.9%). Divers facteurs environnementaux, ainsi que les déplacements des oiseaux suite aux émissions de vocalisations enregistrées, sont confondants pour les estimations de densité des Râles noirs de Californie. Nous avons tenté de contrôler ces biais inhérents, interpolé des indices d'abondance à partir de nos données, et dérivé des classements d'abondance pour les marais représentatifs associés à la Baie de San Francisco et à la côte extérieure. Par rapport à 1986-1988, les taux de détection étaient légèrement supérieurs dans les baies de San Pablo et Suisun, mais étaient plus faibles sur la côte extérieure en 1996. Une analyse des variations entre décennies a suggéré une augmentation des populations des baies de San Pablo et Suisun et une diminution des populations isolées des marais de la côte extérieure ; cependant ces tendances n'atteignaient pas le seuil de significativité. Nous avons mis en évidence une augmentation significative de la probabilité de présence des râles dans un marais avec la taille du marais. Nous avons par ailleurs analysé la relation entre la taille du marais et les indices d'abondance, nous discutons des facteurs qui biaisent les estimations, et nous résumons les facteurs qui influencent probablement la distribution de la population de râles.

Mots-clés: index d'abondance, Râle noir, Californie, *coturniculus*, indices d'abondance, DISTANCE, Baie de San Francisco, marécages de marée, *Laterallus, jamaicensis*.

RÄUMLICHE UND ZEITLICHE VARIATION IN VERBREITUNG UND HÄUFIGKEIT KALIFORNISCHER SCHIEFERRALLEN IN DER BUCHT VON SAN FRANCISCO

Zusammenfassung. Im Jahr 1996 führten wir Erfassungen an 352 Standorten in 26 Flutungsmarschen in der Bucht von San Francisco durch, die einen Vergleich mit Daten von 1986-88 ermöglichen. Die meisten Flächen lagen im Bereich der San Pablo-Bucht ($n = 14$ Marschen, 53.9%), die anderen umfassten Bereiche der Suisun Bucht und dem Carquinez Sund ($n = 5$, 19.2%) bzw. an der Außenküste ($n = 7$, 26.9%). Hochrechnungen des Schieferrallenbestandes werden durch eine Reihe von Umweltfaktoren beeinflusst sowie durch Ortswechsel der Vögel als Reaktion auf den Einsatz von Klangattrappen. Wir versuchten auf systematische Fehler zu kontrollieren, interpolierten Häufigkeitsindizes aus den Daten und ermittelten Häufigkeitsranglisten für einzelne repräsentative Marschen der San Francisco Bucht und der Außenküste. Im Vergleich zu 1986-88 war die Entdeckbarkeit

der Art im Jahr 1996 in den Buchten von San Pablo und Suisun leicht erhöht, an der Außenküste aber geringer. Die Analyse der Bestandsveränderungen über die verschiedenen Dekaden legt eine leichte Zunahme für die Buchten von San Pablo und Suisun nahe, und eine Abnahme für die isolierten Populationen in den Marschen der Außenküste, aber keine der Veränderungen war signifikant. Wir ermittelten eine höhere Antreffwahrscheinlichkeit für die Rallen mit zunehmende Größe der Marschflächen. Schließlich untersuchen wir auch den Zusammenhang zwischen der Größe der Marschen und den einzelnen Häufigkeitsklassen, diskutieren mögliche Fehlerquellen bei der Bestandsberechnung und beurteilen den Einfluss verschiedener Faktoren auf die Verteilung der Rallen in den Untersuchungsgebieten.

Schlüsselwörter: Häufigkeitsindex, Schieferralle, Kalifornien, *coturniculus*, DISTANCE, San Francisco Bucht, Flutungsmarschen, *Laterallus, jamaicensis*.

INTRODUCTION

Tidal marshlands of the San Francisco Bay region support most of the California Black Rail (*Laterallus jamaicensis coturniculus*) population in the western United States (Manolis 1978, Evens et al. 1991). The remainder occur in small, isolated populations in the outer coast tidal marshes (Bodega Bay, Tomales Bay, Bolinas Lagoon, and Morro Bay), freshwater marshes and swales associated with the Colorado River and Salton Sea, and in freshwater marshes of the low Sierran foothills (Repking and Ohmart 1977, Evens et al. 1991, Eddleman et al. 1994, Aigner et al. 1995, Tecklin 1999). However, the latter sites support less than 10% of the total population and, because of fragmentation, they may be susceptible to stochastic extinctions (Evens et al. 1991, PRBO unpubl. data). Former breeding populations in central and south San Francisco Bay and the coastal marshes of southern California have apparently been extirpated (Evens et al. 1991, Eddleman and Evens 1994, Eddleman et al. 1994). The historical and ongoing pressures of agriculture, salt production, and urbanization have reduced tidal marshlands of San Francisco Bay by an estimated 85% (Dedrick 1993), with a concomitant reduction in Black Rail populations (Evens et al. 1991).

In the San Francisco Bay estuary, Black Rails are now confined to remnants of historical tidal marshlands in the northern reaches, primarily those associated with San Pablo and Suisun bays (Manolis 1978, Evens et al. 1991, PRBO unpubl. data). In this study, we surveyed 20 marshes within the estuary and 8 marshes in four embayments on the outer coast. The data obtained were used to compare with earlier

studies, to estimate total population size and to evaluate the status of those populations.

METHODS

Earlier studies (Manolis 1978, Evens et al. 1991, PRBO unpubl. data) determined that in the San Francisco Bay area Black Rails occur almost exclusively in tidally-influenced marshes, in particular, those with unrestricted tidal flow, classified as "estuarine, intertidal, emergent, regularly flooded" (Cowardin et al. 1979, USFWS 1991). In the present study, therefore, we restricted coverage to tidally-influenced marshes.

A total of 27 marsh parcels ranging in size from 9.1 to 149.3 ha (mean = $68.2 \pm \text{S.E. } 8.35$ ha) were surveyed during the period 9 April-28 June 1996. Included were sites that had been previously surveyed in a larger synoptic survey during the period 30 March-2 June 1986-88 (PRBO unpubl. data) (Table 1). Of all sites surveyed, 85% were fully tidal, and 15% were influenced by muted tidal flow. Among marsh parcels surveyed in 1996, 14 (51.9%) were within San Pablo Bay or its major tributaries [mean 73.7 ± 11.02 ha; Dedrick (1993)], five (18.5%) were in the Suisun Bay and the Carquinez Strait (mean 87.7 ± 22.87 ha), and eight (29.6%) were associated with the outer coast (mean 43.29 ± 12.02 ha). Sites in south and central San Francisco Bay were not surveyed because Black Rails were observed at only one of 15 sites in these marshes in 1986-1988 (PRBO unpubl. data). Two sites were sampled on more than one occasion in 1996: Dutchman's Slough (Site # 13, Table 1) on the Napa River and Southhampton Marsh (Site # 17) in Carquinez Strait.

TABLE 1. Summary of the results of 1988 and 1996 Black Rail surveys^a.

Site No.	Location	Stations, n	Marsh size (ha)	Birds/ station 1998 ≤ 30m	Birds/ station 1996 ≤ 30m	A.I. ^b 1998	A.I. ^b 1996	Rank ^c 1996
San Pablo Bay								
1&2	China Camp/Gallinas Creek (S)	24	103	0.10	0.04	0.12	0.09	Low
3.	Gallinas Creek mouth (N)	24	130.4	0.03	0.29	0.07	0.88	Mod
4.	Hamilton Shore	10	39.7	nd	0.00	0.00	0.00	Low
5.	Sonoma Baylands	14.5	100.6	0.70	1.17	1.22	2.89	High
6	Sonoma Creek mouth	13	72.3	0.70	0.31	0.58	0.56	Low
7	Napa Slough	17	54.6	0.61	0.29	0.95	0.71	Mod
8a	Mare Island Point (E)	17	144.2	0.37	0.35	0.90	0.85	Mod
8b	Mare Island Point (NW)	11	36.6	nd	0.08	nd	0.19	Low
9,10	Black John Slough	21	139.2	1.20	1.19	1.53	2.89	High
11	White Slough, Napa River	10	63.9	0.67	0.01	0.97	0.24	Low
12	Wilson Ave, Napa River	07	28.6	0.10	0.00	0.00	0.00	Low
13	Dutchman's Slough, Napa River	04	9.1	1.00	1.25	2.43	3.04	High
14	Coon Island	—	160.3	0.62	nd	1.51	Na	Mod
15	Fagan Slough	20	126.4	0.85	1.58	2.06	3.84	High
16	Bull Island*	09	67.5	0.23	0.11	0.00	0.00	Low
Suisun Bay & Carquinez Strait								
17	Southhampton (Benecia)	12	54.2	0.24	0.92	0.58	1.65	Mod
18	Cutoff Slough (N)	22	115.2	0.26	0.36	0.65	0.85	Mod
19	Cutoff Slough (E)	21	149.3	nd	1.00	1.90	2.55	High
20a	Hill Slough tidal	24	19.6	nd	0.58	nd	1.31	Mod
20b	Hill slough diked*	11	100.0			nd	0.00	Low
Outer Coast								
21	Tomales Bay (south end)	18	45.0	0.30	0.39	1.38	0.95	Mod
21b	Tomales Bay (Tomasini Pt.)	06	~50	nd	0.00	0.00	0.00	Low
21c	Tomales Bay (Bivalve)*	03	~50	nd	0.00	0.00	0.00	Low
22d	Tomales Bay (Ocean Roar)	06	~50	nd	0.00	0.00	0.00	Low
23a	Drakes Bay (Johnson's)	04	~5.0	nd	0.25	0.89	0.69	Mod
23b	Drakes Bay *	06	5.0	0.00	0.00	0.00	0.00	Low
24	Bolinas Lagoon	13	98.0	0.11	0.31	1.10	0.75	Mod
25	Bodega Bay (Doran Park)	15	~5.0	0.00	0.20	0.00	0.49	Low

*Sites with muted tidal flow (as opposed to fully tidal).

^and = no data available; parentheses indicate sites included as part of another parcel. Estimated size is preceded by tilde (~).

^bAbundance indices (A.I.) represent an estimate of the number of birds per hectare as calculated from the number of birds detected per station times the effective census area (36.2 2 m = 0.4115 ha).

^cRank (conforms to Evens et al. 1989): Low = < 0.60 rails ha⁻¹; Moderate (Mod) = 0.60 - 2.12 rails ha⁻¹; High = >2.12 rails ha⁻¹.

Listening stations (aural sampling stations) were located along transects selected to sample elevational change within each marsh and were distributed throughout the length and breadth of the marsh at or above mean high water. Census stations were distributed at 100-m intervals through each marsh parcel and, where possible, each station was at least 50 m from upland habitat. Where possible, listening stations were located at the same sites as the

1986-1988 surveys.

In 1996 a total of 352 listening stations, selected from among the 1108 stations sampled in 1986-1988, were sampled by one observer. Of the stations sampled in 1996, 296 (84.1%) were located in the San Francisco Bay estuary and 56 (15.9%) were located in outer coast marshes. Of the total stations surveyed, 9.1% were in marshes with muted tidal flow. All censuses were conducted between dawn and 0930 hrs

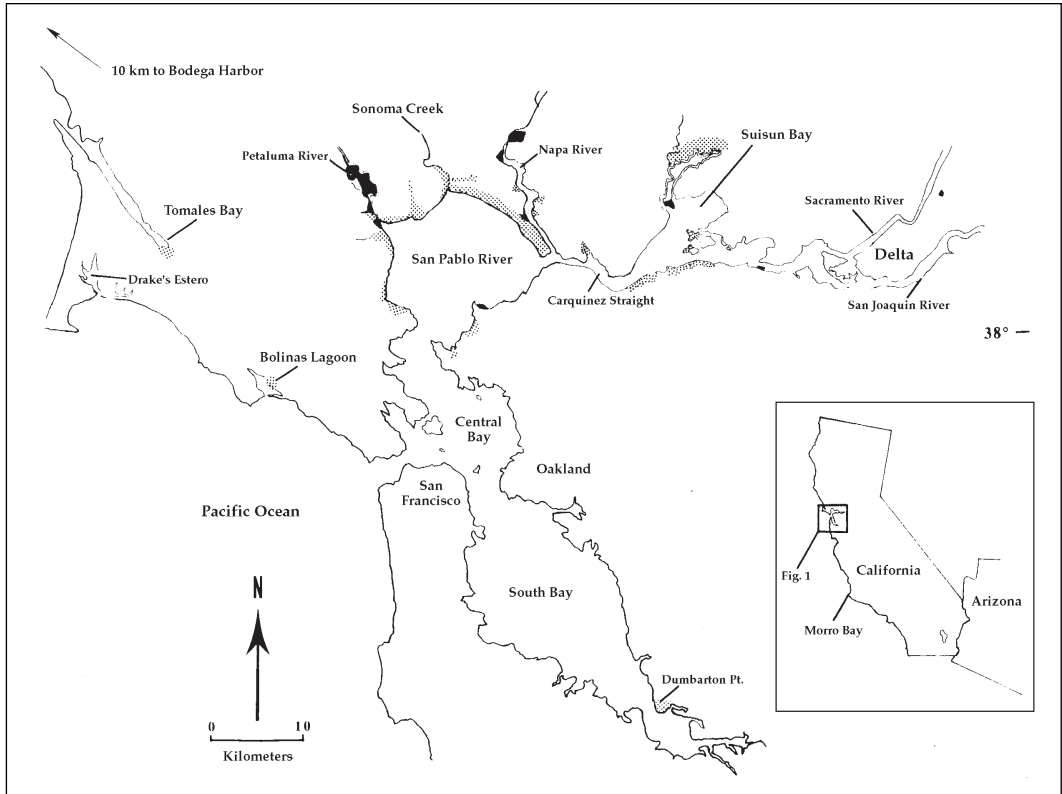


FIGURE 1. Distribution and relative abundance of Black Rails in the San Francisco Bay region. Black shading indicates high abundance; stippling indicates low to medium abundance.

Pacific Standard Time. Census efforts were canceled when wind exceeded approximately 25 km hr^{-1} or when the observer determined that background noise was interfering with the ability to detect rail vocalizations. After arriving at a listening station, the observer waited silently for one minute then broadcast a tape recording of California Black Rail vocalizations in each ordinal direction for a total of 1.5 min. The tape recording consisted of a repetitive series of *grr* calls followed by 0.5 min of *kik-kik-kerr* calls (Repking and Ohmart 1977, Eddleman et al. 1994). Maximum sound pressure 1 m from the source was approximately 90 dB. Each station was sampled for a total of 6.0 mins.

For each rail response heard within 5.0 min of initiating the broadcast, the observer recorded the time, the call type, and the estimated distance and direction from the center of the station. An effective 30-m census radius was chosen after field testing found that the

observer's ability to estimate distance accurately, or hear low range vocalizations consistently, declined beyond that distance. This protocol also conformed with earlier studies (PRBO unpubl. data, J. Tecklin pers. comm.). All calls coming from one compass direction during the five-minute listening period were considered to represent only one rail unless two calls were heard simultaneously. Calls from different ($>30^\circ$) compass directions were considered to represent different rails. In an earlier study it was estimated that Black Rails move toward the source of a broadcast tape an average of 6.2 m (PRBO unpubl. data); therefore, although we counted birds only within 30 m of the observer, we calculated abundance indices assuming that the effective radius of sampling stations was 36.2 m, thus covering an area of 0.412 ha (Table 1). The movement of Black Rails in response to the playback of vocalizations potentially confounds extrapolation of densities. Spear et al.

TABLE 2. Abundance indices and population estimates of Black Rails for each region. Abundance index is number of rails detected per effective census area (see Table 1). Population estimates are shown with and without adjustment for detection probability and amount of suitable habitat (see text).

	Habitat Size (ha)	Median Abundance Index \pm S.E.	Median Abundance Index	Sites, n	Abundance Estimate based on Median ^a	Adjusted Abundance Estimate ^b
San Pablo Bay	5531	1.25 \pm 0.345	0.71	13	3,930	7,100
Suisun & Carquinez	3780	1.43 \pm 0.320	1.08	5	4,080	7,200
Outer Coast	543	0.46 \pm 0.196	0.30	5	163	289

^aEstimated number of Black Rails per region based on median abundance index only, not adjusted for detection probability or suitability of habitat.

^bEstimated number of Black Rails per region, incorporating detection probability of 0.33 (from DISTANCE, see text) and assumption that not all habitat is suitable for Black Rails (see text).

(1999) used our correction factor and found a high degree of conformance with expected detection values (*contra* Legare et al. 1999).

Abundance indices calculated for each marsh assumed complete detectability within 36.2 m of the observer (see below), and thus provide a lower-bound estimate of abundance. Abundance rankings were assigned to each site based on the density index calculated from the 36.2 m radius circular plot as follows: <0.6 rails ha⁻¹ (low); 0.6-2.1 rails ha⁻¹ (moderate); >2.1 rails ha⁻¹ (high). This scale conforms to our earlier analyses (PRBO unpubl. data).

The values derived from the average number of detections per hectare in each marsh parcel were also used to calculate abundance indices for each region. We then used these abundance indices to extrapolate total abundance estimates for each region. Because these estimates rely on extrapolated data, we acknowledge the considerable uncertainty associated with any estimates of absolute abundance.

To address the problem of incomplete detectability (i.e., detectability less than 100% within the survey station radius), we used the program DISTANCE (Buckland et al. 1993). The program used information regarding the distance at which each rail was detected (up to a distance of 30 m) to estimate true detection probability. Model selection in DISTANCE was conducted using the Akaike Information Criterion (AIC; Buckland et al. 1993). A second consideration we took into account in estimating absolute population size was the amount of tidally-influenced marsh habitat that was truly

suitable for Black Rails. We derived estimates of the fraction of suitable habitat and then combined that estimate with the estimate of rails present but not detected in our surveys in order to derive adjusted regional estimates of total Black Rail population size.

RESULTS

RELATIVE ABUNDANCE

Abundance Indices (number of rails detected per census area) are presented in Table 1 for each marsh surveyed in 1996 (with comparison to 1988 results), assuming a detection radius of 36.2 m (see Methods). These abundance indices assume complete detectability of rails (for which, see Below) and are thus minimum estimates. We summarize relative abundance for each region, presenting both the mean (\pm S.E.) and median abundance index, in Table 2. The arithmetic mean was particularly sensitive to extreme low values and thus we feel the median is a better measure of the central tendency. These summary statistics included two San Pablo Bay sites and four outer coast sites with no detections, but did not include sites of muted tidal flow.

Results indicated statistically similar indices in San Pablo Bay compared to the Suisun Bay and Carquinez Straights region (Table 2). It may seem that Suisun Bay abundance values were somewhat higher (1.08 vs 0.71 for median values), but any such difference is unreliable for two reasons. First, only a few marshes were surveyed in Suisun Bay (compared to San Pablo

Bay), and sampled marshes may not be representative of the region as a whole. Second, marshes in Suisun Bay were selected because we knew, or expected, rails to occur there. In contrast, marshes of San Pablo Bay were not selected *a priori* with respect to the known presence of rails; also, we omitted the Petaluma River marsh, a site within San Pablo Bay that is known to support very high densities of Black Rails, from this analysis.

We emphasize that the primary objectives of the surveys were to compare abundance indices in 1996 with those from the 1980s and to compare marshes within a region, not to compare among regions. Also, we sampled only large, broad marshes in the Suisun system, whereas an unknown proportion of the Suisun marshland was comprised of linear strip marsh along sloughs.

BETWEEN YEAR AND BETWEEN DECADE VARIATION

We selected 16 study sites where rails were present and for which data were available from 1988 and 1996 and using these sites, compared abundance indices to determine whether there was interannual variation. The mean 1988 abundance index was 1.08 (\pm 0.16); the 1996 mean was 1.46 (\pm 0.29), suggesting a population increase of 35% within these 16 sites, but one that is not significant (*t*-test on log-transformed abundance indices). Indeed, if we consider only the largest six marshes (>100 ha) with full tidal influence from all regions for which we have data from both years, we find a mean abundance index of 1.98 (\pm 0.53) rails ha⁻¹ in 1996 as compared to 1.19 (\pm 0.32) rails ha⁻¹ in 1988, an increase of 66%, a difference which is also not significant (*t*-test on log-transformed values).

Another measure of interannual variation is contained in the detection fraction, i.e., the percentage of stations at which rails are detected within a marsh. In an earlier survey of San Pablo Bay marshes, Black Rails were detected at only 0.240 of the 338 stations sampled (PRBO unpubl. data) whereas in this study we detected rails at 0.470 of 212.5 stations sampled. In Suisun and Carquinez we detected birds at 0.254 of 114 stations in 1988; in 1996 we detected birds at 0.568 of 56 stations. On the Outer Coast, the rate is not available for the 1988 surveys, but in 1996 the response rate was 0.146 at 56 stations.

Although temporal variation in abundance was suggested from the difference in mean number of detections per station from 1988 to 1996, it did not cross the threshold of significance. A matched pairs *t*-test, using logs of abundance indices of all sites with detections (i.e., marshes with no detections eliminated), failed to reject the null hypothesis that there was no difference between years ($P > 0.3$). When the Outer Coast sites were excluded, the tendency toward increase from 1988 to 1996 was still not significant ($P > 0.15$).

REGIONAL DIFFERENCES

Our data suggested between-decade differences in abundance indices among the three regions. In Suisun Bay all three marshes that were covered in both survey years showed higher abundance indices on the later surveys. In San Pablo Bay, five increased, two decreased and the remainder were virtually unchanged (i.e., absolute change <0.05 rails ha⁻¹; Table 1). On the outer coast, three sites at which rails were present in 1988 showed a decrease in 1996. One, Bodega Bay, showed an increase. In fact, Bodega Bay was apparently colonized in the intervening years. Marshes in all regions that showed declines from 1988 to 1996 were generally small, relatively isolated from one another, and isolated from large Black Rail population centers.

A comparison of abundance indices in Table 1 also reveals that, with the exception of Bodega Bay, no marsh that had zero detections in 1988 was observed to have rails in 1996. Thus, the relatively isolated Bodega Bay site was the only 'empty' marsh that was apparently colonized in the intervening years. Conversely, all but one marsh with rails in 1988 contained rails in 1996. The marsh that held rails in 1988 but was without detections in 1996 (Site 12; Table 1) had only one bird in the earlier survey and rails have been detected there subsequent to 1996 (J. Evens, pers. obs.), therefore the difference between years was likely due to census error. Thus, no local extinctions were detected among the two time periods.

RELATIONSHIP BETWEEN MARSH SIZE AND ABUNDANCE INDICES

There was a tendency for abundance indices to increase as size of the marsh increased ($P = 0.054$, regression analysis of log-transformed

abundance on marsh area, ha). To clarify whether or not abundance values were indeed related to marsh area, we partitioned abundance values into two components: (1) presence of rails in a marsh (value >0), and (2) abundance indices of rails, given that rails were present in the marsh (one or more detected). To examine the first component, we classified each marsh with respect to presence (score = 1) or absence (score = 0) of rails. When results from all regions were combined, there was a significant positive relationship between marsh size and presence of rails (Likelihood Ratio Statistic = 4.38, $df = 1$, $P = 0.036$). When San Pablo Bay, the region with the greatest number and size diversity of study sites was analyzed by itself, marsh size was also significant with respect to the presence of rails ($P = 0.034$).

For the second component, there was a positive trend for the abundance index to increase with increasing marsh size among marshes with rails (when analyzed by region and overall) but this was not significant ($P > 0.3$ for all four analyses). We conclude that marsh size influences the likelihood a marsh will contain rails, but it is unclear whether further gradation in Black Rail abundance is influenced by marsh size.

ABSOLUTE ABUNDANCE AND POPULATION ESTIMATION

Reliable estimation of absolute abundance requires consideration of two factors: 1) detectability of rails (proportion of rails detected within each effective census area) and 2) proportion of habitat suitable for rails. To assess the first factor, we analyzed distances at which rails were detected using the program DISTANCE (Buckland et al. 1993; see above) for observations of individuals within 30 m of the observer. Using a uniform density function with polynomial adjustments, detection probabilities were estimated to be 100% at 3 m, 75% at 5 m, 25% at 10 m, and 5% at 30 m. From this we conclude that substantial numbers of rails were being missed in our surveys. It was not possible to estimate detection probabilities on a per-marsh basis. Instead, we assumed the same detection probability function at all marshes and estimated abundance in each marsh.

For San Pablo Bay, the median detection value, as determined by DISTANCE, for the 14

marshes was 2.13 birds ha^{-1} , after adjusting for estimated bird movement toward the observer (i.e., assuming an effective radius of 36.2 m). This value is 3.0 times the median density when assuming complete detectability (Table 2). In other words, observers were detecting only 33% of rails within 36.2 m of observers. We, therefore, adjusted relative abundance estimates by a factor of 3.0 for all Bay regions, for the purpose of estimating absolute abundance.

The extent of truly suitable habitat in the Suisun Bay and San Pablo Bay regions is likely as little as 50% to 75% of the area represented by Dedrick's (1993) estimate (3,780 ha). For San Pablo Bay and Suisun bays we therefore estimated that 65% of the area is suitable habitat. For the Outer Coast, we estimate the percent of suitable habitat to be 50% (due to vegetational differences and increased edge effect) compared to San Francisco Bay.

Finally, we incorporate both the estimated fraction of truly suitable habitat within nominally-designated tidal marshland and detectability of rails, to derive estimates of total population size (Table 2). We estimate approximately 7,200 Black Rails in the San Pablo Bay system and a similar number in Suisun Bay and Carquinez Strait, with about 290 Black Rails in the Outer Coast region. However, we note that there are several other sources of bias that might reduce or inflate our estimates by an undetermined amount (see "Factors that may bias estimates," below.)

DISCUSSION

Factors that may bias estimates or obscure interpretation of results

(1) In San Francisco Bay, Black Rails tended to occur in the larger undiked marshes associated with larger rivers and in some bayshore parcels, particularly those associated with the mouths of rivers or creeks (Evens et al. 1991). Dedrick's (1993) estimates of areal extent of marshland habitat, upon which our area estimates are based, includes an as yet unknown proportion of narrow strip marshes, bayfront marshes not associated with tributary mouths and low *Spartina* or *Scirpus robustus* beds, none of which support Black Rails. We estimate that those habitats may account for 35% of the tidal marshlands of San Francisco Bay, but these

estimates are very rough.

(2) We have accounted for the movement of birds toward the observer based on observed (estimated) movement after first detection; however, we have no way of knowing whether birds move prior to their initial call, but suspect they do (see Legare et al. 1999). In effect, the tape may be acting to lure birds in from a larger area. Hence, true densities may be lower than the abundance indices reported herein.

(3) The age at which calling begins is unknown. It is possible that detections after mid-May include juvenal birds, not just adults.

(4) Little is known regarding the sex-related vocalizations of this race of Black Rail (but see Legare et al. 1999 in reference to *L. j. jamaicensis*). It is presumed that the *kik-kik-kerr* call is most often given by the male (Eddleman et al. 1994, Legare et al. 1999), but less than 10% of our detections within 30 m of the observer were of this type. Approximately 90% of the detections in this and previous studies of *L. j. coturniculus* were "growl calls" (*grr*) in response to broadcast tapes, and it is not likely that these agitated "scolding" vocalizations represent only territorial males (PRBO unpubl. data, Eddleman et al. 1994, Legare et al. 1999). The broadcasts may well elicit responses from nesting females. Indeed, in reference to *L. j. coturniculus*, Flores and Eddleman (1993) state that "scolding occurs in response to disturbance while female is displaying near nest site." Because of these uncertainties we can not say whether our values represent just territorial males or some fraction of the total number of breeding adults of either sex. The findings of Legare et al. (1999), with *L. j. jamaicensis* in Florida indicated that on average only 50% of males and 20% of females responded.

(5) Spear et al. (1999) tested the effects of temporal and environmental factors on the probability of detecting California Black Rails and found that they explained 15-20% of the variation in detection probability. Through our methodology we controlled or attempted to control most of those factors (survey timing, tide height, air temperature, wind speed, cloud cover), but we did not consider moon phase.

(6) Finally, this study was a synoptic survey with sites chosen to represent the geographic breadth of tidal marshlands in the northern reaches of the San Francisco Bay area. Therefore,

sites were fairly well distributed along varying reaches of watercourses and at representative marsh types (bayshore, river or slough shore, river mouth). However, there was probably some bias because certain sites were more accessible than others. Higher marshes are more easily accessed by observers and although all stations were above mean high water, stations were probably located within the higher portions of the available elevational gradient. Although we attempted to use straight transects, observers often had to modify their route because large sloughs impeded movement toward the lower marsh plain where sloughs widen.

ABUNDANCE ESTIMATES AND VARIATION IN ABUNDANCE

Keeping the above caveats in mind, it is clear that it is difficult to precisely estimate Black Rail abundance at this time. Our best estimate based on current methodology is about 14,500 Black Rails in the entire San Francisco Bay system, with a lower-bound estimate of 8,000 Black Rails; however, the true number may be higher or lower, depending on the factors listed above. As estimates of percentages of appropriate habitat and estimates of rail movement in response to tape playback and sex-related frequencies are refined, the confidence of our abundance estimates will improve or require reevaluation.

FACTORS INFLUENCING ABUNDANCE

The apparent increase in total population observed in some regions in this survey could have been related to variation in the hydrologic cycle. The 1988 surveys followed two relatively dry seasons. In contrast, in 1994-95 and 1995-96 rainfall was above normal. Perhaps more importantly, both years preceding this study experienced anomalous spring precipitation (18.1% of the annual rainfall in 1995-96 fell in April and May). It is well-known that rails favor marshes where the substrate is saturated (Eddleman et al. 1994) and the results of this study suggest that marshes that are isolated from tidal influence, or that receive muted tidal flow, may provide Black Rail habitat only in years of high rainfall.

In contrast, outer coast marsh abundance indices showed a strong tendency to decline,

which is of great concern since abundance values were already lowest in these marshes. The long-term outlook for these marshes is bleak, although a tidal marsh restoration project in Tomales Bay (National Park Service) aims at more than doubling the available outer coast rail habitat in the future.

It is not surprising that abundance patterns (overall difference and differences in time trends) differed between Suisun and San Pablo bays, because these bay regions are somewhat dissimilar (Goals Project 1999). The Suisun system is less saline than San Pablo and Black Rails prefer some freshwater influence both among and within marshes (Evens et al. 1991, Eddleman et al. 1994). In addition, predator pressure likely differs among regions, with the less urbanized Suisun Bay supporting a different complex of mesopredators than the more urbanized San Pablo Bay. Another factor influencing Black Rail abundance (for which we have little information) is diversity of habitat relative to tidal level on a micro-scale. Low elevation areas are susceptible to inundation, increased predation (Evens and Page 1986) and nest loss (Eddleman et al. 1994).

RELATIONSHIPS BETWEEN RAIL PRESENCE, ABUNDANCE AND HABITAT VARIABLES

In an earlier study, vegetation height, presence of *Frankenia* (an indicator of high elevation marsh habitat), and absence of amphipods (indicators of lower elevation marsh) were identified as key predictive factors in Black Rail distribution (PRBO unpubl. data). Observational data suggests also that the condition of transitional vegetation along the upland edge adjacent to marshes is a factor in habitat suitability for rails (Evens and Page 1986). Subsequent field work, including this study, has suggested other variables that help explain the patchy distribution of San Francisco Bay region tidal marshes (Flores and Eddleman 1993, Evens et al. 1991): marsh size, marsh distribution (contiguity), marsh configuration (linear vs broad), predator populations, hydrological cycles, and fluctuations in water level.

1) Size. This study indicates that marsh size may be positively correlated to an increase in rail abundance. Smaller marshes are less likely to support rails and there is a non-significant but positive tendency for abundance and density to

increase with marsh size. This tendency is exhibited in each region. That said, it is important to recognize that Black Rails can utilize very small patches, especially in areas where large patches are unavailable (Aigner et al. 1995, Tecklin 1999, J. Tecklin pers. comm.).

2) Contiguity. We did not systematically evaluate the contiguity of marshes in San Francisco Bay, however, it is likely that the distributional relationship of each marsh to other marshes influences presence or absence as well as relative abundance of rails. At some sites (e.g. Rush Creek/Black John Slough), we observed occupation by rails of marshes with muted tidal flow if they were adjacent to a fully-tidal marsh and the substrate was hydrated (i.e. in a wet year), but not flooded.

The Rallidae in general disperse effectively (del Hoyo et al. 1996) and the apparent colonization of several disparate and isolated sites in California in recent years (Evens et al. 1991, Aigner et al. 1995, Tecklin 1999, J. Tecklin pers. comm.) suggests that this is the case for Black Rails as well. In addition, the most isolated marsh within the San Francisco Bay system — Southhampton Marsh in the Carquinez Strait — supports an apparently persistent population (at least since 1988 — authors, pers. obs.). From a rail's perspective, the marshes of San Francisco Bay are perhaps all contiguous.

3) Configuration. Although for the purposes of this study we did not quantify linearity versus breadth of each marsh, we have observed that broader marshes tend to support rails (and in higher abundances) than linear marshes. Thus, rails are very sparsely distributed along the narrow strip marshes that fringe many of the larger watercourses in San Francisco Bay (e.g. Napa River) but tend to be concentrated in broader patches. This pattern is perhaps a manifestation of what is generally displayed in the area relationships, i.e. a function of ratio of edge to 'center,' as well as the geophysical effect of elevational gradients being compressed in linear habitats (i.e. along tidal sloughs) and, therefore, less elevational gradient is available. (In an intensive study of Sonoma Creek Marsh, in 1987, we documented distribution within a linear marsh that mirrored the microelevational changes within the marsh; authors, unpubl. data).

4) Predator populations. Sites bound by levees or rip rap provide access and habitat to mammalian predators and, therefore, predation pressure may increase at those sites, especially when peripheral vegetation does not provide refuge. Some sites are crossed by boardwalks or pathways, increasing vulnerability of resident rails to these predators. Predator populations also vary among regions within the San Francisco Bay area.

5) Hydrology. As described in an earlier study (Evens et al. 1991), within the San Francisco Bay region tidal marshes that are subjected to fully tidal influence provide the best habitat for Black Rails. Within those marshes, particularly in younger sites or those sites that have suffered extensive hydrological modification by humans (mosquito ditching, etc.), the rails may be clustered near sources of fresh water influence as indicated by "*Scirpus* islands." These habitat features are not necessarily natural and may have become established as the result of drainage modification, e.g. culvert outflows. This pattern of distribution (evident at China Camp, Mare Island, and several other sites) mirrors the situation as described at some sites in the Sierra foothills (Tecklin 1999) and along the Colorado River and Imperial Canal (Repking and Ohmart 1977, PRBO unpubl. data), sites at which rails are associated with freshwater leaks in water transport systems.

6) Water levels. Fluctuation of water levels is one of the habitat variables that determines presence or absence of Black Rails (Flores and Eddleman 1991, Evens et al. 1991, J. Tecklin pers. comm.). Inundation above a certain depth may exclude habitat to Black Rails; if the inundation is periodic and short-lived (e.g. tidal), and there is upland refugia adjacent to the marsh, rails may persist at the site.

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