HABITAT USE BY CLAPPER RAILS IN THE LOWER COLORADO RIVER VALLEY

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ABSTRACT.—Densities of the Clapper Rail (*Rallus longirostris yumanensis*) were determined in marshy situations in the lower Colorado River valley in all seasons. We conducted a study to quantify environmental variables important to rails within censused areas along the 450 km of the lower Colorado River north of Mexico in order to learn more about their year-round habitat requirements. Quantified vegetation variables from 40 marsh areas were subjected to principal components analysis; four principal components collectively accounted for 75% of the variance.

Habitat breadths of rails were broadest in summer and narrowest in winter. Marshes with the highest rail densities in one season tended to have large rail densities year-round. The converse was true for marshes with low densities.

In the first of two analyses, 27 of the marshes (each censused monthly for two years) were used to determine rail associations with the vegetation principal components (PCs). Spearman rank correlations of rail densities with PCs revealed that rails were associated primarily with dense marsh vegetation (PC I) at all seasons. This outcome was tested and confirmed with data from 13 marshes censused during summer 1976 that were not included in the first analysis.

One reed (*Phragmites australis*) and two cattail (*Typha domingensis*) marshes of moderate foliage density consistently had more rails than expected. One dense cattail marsh consistently had fewer rails than expected. Size of marsh (2-29 ha) and bank slope into the water were apparently unrelated to density of rails per 10 ha.

Censuses from this and unpublished recovery team studies suggest a rail population of about 750 birds for the lower Colorado River north of Mexico.

The Yuma Clapper Rail (Rallus longirostris yumanensis), restricted to the lower Colorado River drainage system and the Salton Sea in the Imperial Valley of California, is considered an endangered species by the U.S. Fish and Wildlife Service (USFWS). Its numbers have been closely monitored because marsh habitat required by this species is only moderately abundant. In 1972, the USFWS established the Yuma Clapper Rail Recovery Team, which has since annually censused the breeding population along the lower Colorado River. These censuses did not include any quantification of the environmental variables associated with rail densities. Knowledge of the habitat requirements of rails comes largely from detailed, very local, single-year studies with emphasis on the breeding season. Such studies were conducted at Topock Marsh near the northern limit of the range of the Clapper Rail (Smith 1975) and at the western edge of the Salton Sea (Bennett and Ohmart 1978).

Studying the habitat of the Clapper Rail over a large portion of its range is important because habitat relationships found in local areas can differ substantially from those over much larger (regional) areas (Wiens 1981). Habitat relationships found by Bennett and Ohmart (1978) differed markedly from those found by Smith (1975). The rails in those studies inhabited stands of bulrush (Scirpus spp.) or cattail (Typha spp.) in differing degrees. We know of no studies about their use of other vegetation associated with marshes, such as reed (Phragmites australis), loosestrife (Lythrium californicum), and various grasses. In view of the endangered status of the Clapper Rail, data concerning habitat relationships over the entire area are necessary to properly manage the population. Since relationships between various bird species and the vegetation often change seasonally and annually (Rice et al. 1980; Laurenzi et al. 1982; Meents et al. 1982, 1983), data from as many seasons and years as possible should be included when attempting to clarify the relationship between a species and its habitat.

In our study we examined Clapper Rail use of marsh habitat along the lower Colorado River for several seasons over a period of three

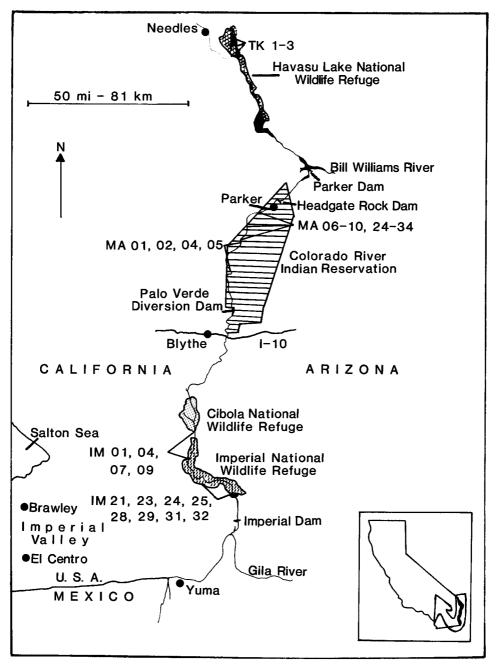


FIGURE 1. Map of the lower Colorado River north of Mexico. Study areas are designated with prefixes of IM, MA, and TK.

years. Censusing included marshes scattered over the Colorado River from Davis Dam to the Mexican border. Our results are based on more than 2,000 censuses and 1,100 detections of Clapper Rails.

METHODS

Line transects were established in 40 marsh areas along the lower 450 km of the lower Colorado River valley (Fig. 1, Appendix 1) and were censused three times each month using a modified (Anderson and Ohmart 1977) Emlen (1971) technique. Some transects were established routes through marshes and were censused by boat. Other transects followed jetties or dikes. We always censused in the morning, beginning at sunrise in spring, summer, and fall, and at one hour after sunrise in winter. Censusing continued for approximately two hours, generally corresponding to the time when rails were most active (Anderson and Ohmart 1977). We either censused each area

Variable	PC I	PC II	PC III	PC IV
Total foliage density	0.960	0.214	-0.001	0.002
Density at 0.15 m	0.932	-0.175	-0.051	0.164
Density at 0.6 m	0.902	0.346	0.007	-0.004
Density at 1.5 m	0.802	-0.409	-0.033	0.108
FHD	0.597	-0.156	-0.237	0.232
Grass	-0.598	0.097	0.453	0.479
Trees	-0.348	0.065	0.729	-0.226
Reed	0.241	-0.844	-0.028	0.012
Bulrush	0.226	0.435	0.129	0.647
Cattail	0.132	0.576	-0.564	0.149
PI	-0.097	0.007	-0.628	-0.047
Loosestrife	0.024	0.248	0.288	-0.764
Percent variance				
accounted for	37	16	12	10

TABLE 1. Loadings of each vegetation variable on four principal components (PCs).

at the beginning, middle, and end of the month or concentrated censusing in the middle of the month. Since several census-takers were involved, they were assigned areas on a rotational basis in order to minimize variation in population estimates due to slight differences in the abilities of different censusers. Months were grouped into seasons, based on changes in rail populations. Seasons included winter (November–February), spring (March and April), summer (May–July), and late summer– fall (August–October).

We divided each transect into 150-m sections. Foliage measurements were taken at 15 m from each end and in the middle of each section on each side of the transect. Foliage density (DEN) was measured using the board technique (MacArthur and MacArthur 1961). Foliage height diversity (FHD) was computed from relative foliage density estimates using information theory (Shannon and Weaver 1949). We determined patchiness (PI) from the sum of the variance of the average foliage density taken at various heights in the 150-m plots (Anderson et al. 1978, Meents et al. 1981). Each plant species' contribution to community composition was assessed by first counting the number of points where vegetation measurements were taken. We tabulated particular plant species (e.g., cattail [Typha domingensis], reed, various species of trees and grasses, and loosestrife) occurring at each point. The number of points of occurrence was converted to a proportion by dividing by the total number of points. Measurements, usually made in May or June and August or September, were used to characterize each transect for all months of that year under the rationale that measurements of green foliage in summer generally represented density of dead vegetation in winter. This assumption was validated by field measurements from selected sites (Anderson and Ohmart, unpubl. data).

Vegetation variables (Table 1) were subjected to principal components analysis (PCA) to determine the number of independent vegetation trends (principal components [PCs]). Each PC includes highly intercorrelated variables from the original set. These highly intercorrelated variables can be used to characterize the PC, but we emphasize that all variables contribute to all PCs. Each transect received a factor score, usually ranging from approximately 3.0 to -3.0 for each PC. A positive score indicated that the transect was above average for the constellation of variables that characterized a given PC.

The rail data were divided into two parts. The first included two years (1977–1978) of monthly data from 27 marshes, and the second included density estimates for summer 1976 for 13 marshes not included in the first analvsis. We combined (for both years) the monthly density estimates for each month within a season. Transects were then ranked from highest to lowest rail count. Transect vegetation factor scores were also ranked from highest (positive) to lowest (negative) for each PC. Rail numbers were compared with the rank order of the transect factor scores using Spearman rank correlations (Siegel 1956). Rails could be associated with the vegetation represented on more than one of the PCs, so to check this possibility, we simply added the factor scores of two or more PCs. Further, it was possible for rail numbers to be associated positively with one PC but negatively with another. To check for such relationships, we simply changed the sign on one set of factor scores before adding the two PCs together. All possible comparisons were made. This increased the possibility of Type I error, but the outcome was tested in other ways; thus, consistency was more important than any single statistically significant outcome.

In our previous work, we found that rela-

		Significance					
Season	Habitat breadth	Winter	Spring	Summer	Fall		
Winter	0.639		< 0.001	< 0.001	< 0.001		
Spring	0.990	0.767***	_	< 0.001	< 0.001		
Summer	1.251	0.432*	0.647***	_	< 0.001		
Late summer-							
fall	1.150	0.656***	0.605**	0.575**	_		

TABLE 2. Seasonal changes in habitat breadth and significance of differences (above diagonal) and correlation of ranked densities across seasons (below diagonal).

tions between wildlife and vegetation often were not linear (Meents et al. 1981, 1983; Anderson et al. 1983). In this study, we checked for certain non-linear relationships by using factor scores raised to the second and third powers. Non-linear relationships were not found. From the correlation analyses of the first data set, we obtained significant correlations between rail numbers and certain habitat variables. We tested predictions of rail habitat use derived from the first data set by comparing them with the second data set. The prediction was that the same rail-habitat associations would be apparent, using the test set of marshes.

Seasonal distribution (habitat breadth) among the 27 transects in the first analysis was characterized with information theory (Shannon and Weaver 1949). Differences in distribution (H') between seasons in habitat breadth were tested with a *t*-test (Zar 1974).

Even though habitat breadth may change seasonally, it seemed possible that certain areas that were preferred in one season might be preferred in all seasons, and that at least some areas without rails in one season would have no rails in all seasons. We investigated this possibility by using a Friedman two-way analysis of variance (Siegel 1956).

RESULTS

VEGETATION ANALYSIS

Principal components analysis of the vegetation data yielded four PCs (those with eigenvalues ≥ 1.0), which accounted for 75% of the variance in the total data set (Table 1). PC I accounted for 37% of the total variance and ordered transects along a trend from low-tohigh foliage density. Foliage density at 15 cm did not load as much on this trend as density at other levels. None of the individual plant species loaded heavily on this PC, indicating that foliage density of particular plant species did not closely parallel this trend. Thus, a dense stand of cattail with no bulrush or reed present. or a dense stand of bulrush in the absence of the other two plant species, resulted in the lack of correlation of any of these species with PC I. Where trees were most abundant, total foliage density tended to be somewhat lower than average, as indicated by the negative loading by trees on PC I (Table 1).

PC II described a trend from transects with abundant reeds (maximum height: 3 m) and few cattail or bulrush, to transects with vegetation consisting of rather short bulrush and cattail and no reeds. This PC accounted for 16% of the variance, while PC III accounted for 12% of the variance. Transects loading heavily on this PC had a relatively high proportion of points with trees and grass but few cattail or little horizontal patchiness. The final PC, explaining 10% of the variance, described a trend from transects with a relatively large proportion of points with bulrush and grass (positive loadings) and few loosestrife, to transects with abundant loosestrife (negative loadings) and few reed or bulrush.

HABITAT USE

Habitat breadth. Habitat breadth differed significantly among all seasons (Table 2), being narrowest in winter and broadest in summer.

Correlations between seasonal distributions. Significant Spearman rank correlations in all seasonal comparisons indicated that areas used and not used in one season were correspondingly used or not used in compared seasons (Table 2). Similarity in use was weakest between summer and winter. The tendency for used and not used areas to be the same across all seasons (Friedman's test) was significant $(\chi^2 = 48, df = 25, P < 0.01)$. Among the six highest ranking transects each season were three transects that were in this category every season (Table 3). If peak abundances were randomly distributed among the 27 transects, the probability of a single transect being among the top six transects for each of four seasons is P = 0.006 (Table 3). The probability of three such transects occurring by chance is infinitesimally small. In addition, three transects were among those with the lowest density ranks each season. The probability of this occurring

^{*} P < 0.05. ** P < 0.01. *** P < 0.001

TABLE 3. The six transects ranked highest for Clapper Rail densities (\times) and those with no Clapper Rails or with the six lowest ranks (O).

					T	otal
Transect	Winter	Spring	Summer	Fall	Top six	Bottom six
IM-01	0	0	×		1	2
IM-04	00		×	×	2	1
IM-07	0		×		1	1
IM-09	0			0	0	2
IM-21	0	×			1	1
IM-23	×				1	0
IM-24	×	×			2	0
IM-25	×	×	×	×	4	0
IM-28	×	×	×	×	4	0
IM-29	×	×	×	×	4	0
IM-31	×	×		×	3	0
MA-04	0				0	1
MA-05	0				0	1
MA-21	0	0		0	0	3
MA-22	0		×	000	1	2
MA-23	0	0	0	0	0	4
MA-24	00000	0			0	2
MA-25	0	0	00		0	3
MA-26	0	0	0		0	3
MA-27	0	0			0	2
MA-28	0	0		×	1	2
MA-29	0	0	0	0	0	4
MA-30	0	0		00	0	3
MA-31	0	0	0	0	0	4
MA-32	0	0	0		0	3
MA-33	000000000	000000000000000000000000000000000000000			0	3 2 4 2 3 3 2 2 4 3 4 3 2 3
MA-34	0	0		0	0	3

by chance for a single transect, because of ties, was not statistically significant (P = 0.073), but the probability of this occurring for three transects by chance alone was highly unlikely (P < 0.001).

VEGETATION VARIABLES ASSOCIATED WITH CLAPPER RAIL DENSITIES

Winter. In winter, Clapper Rails were found on six transects. Their distribution was significantly ($r_s = 0.678$, P < 0.001) correlated with foliage density (PC I, Fig. 2). Because these transects were located primarily at the south end of the study area, we standardized the latitude of each transect, added these values to PC I to obtain a new set of values, ranked them, and did another correlation. The rank correlation then increased to $r_s = 0.740$. This adjustment strengthened the conclusion that the small population was associated with dense vegetation in the southern parts of the study area. The rails tended to be associated with areas that had a greater proportion of points with trees nearby $(r_s = 0.578)$, but this was not significant (0.2 > P > 0.1).

Spring. In spring, the rank order of rail densities was associated with PC I (Fig. 3). Three transects (ranked vegetationally as 16, 20, and 23 on PC I) had substantially more rails than expected. In addition, the transect ranked 24

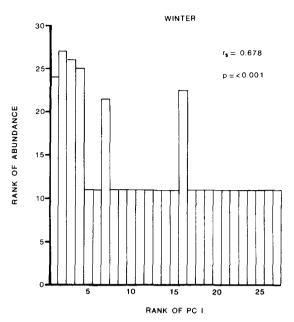


FIGURE 2. Correlation between ranks of densities on transects with ranks of transects on the first principal component from the vegetation analysis during winter. Densities were ranked on the graph so that the largest density received the largest rank. The smallest loading on PC I was given the smallest rank. Thus the largest rail densities are associated with the largest transect score on PC I.

had more rails than expected even though there were only 2 rails/40 ha. Among the transects ranked 16, 20, and 23, two were marshes with clumps of dense to moderately dense cattail interspersed with open water; the other (transect ranked 23) was a dense stand of reed.

Summer. In summer, ranks of rail densities were correlated with dense vegetation (PC I),

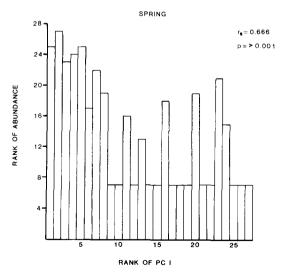


FIGURE 3. Correlation between ranks of Clapper Rail densities on transects with ranks of transects on the first principal component from the vegetation analysis during spring. Ranks of densities arranged on vegetation ranks as in Figure 2.

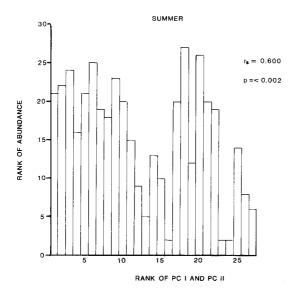
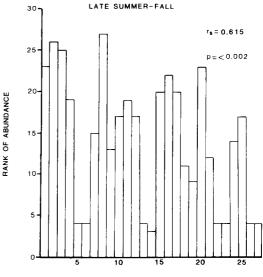


FIGURE 4. Correlations between ranks of Clapper Rail densities on transects with ranks of transects on the first two principal components combined from the vegetation analysis during summer. Ranks of densities arranged on vegetation ranks as in Figure 2.

but the correlation ($r_s = 0.405$, P > 0.05) was low. Ranks were correlated with sparse cattailbulrush marshes ≤ 1 m tall (PC II) at about the same level ($r_s = 0.384$, P > 0.05). By combining PC I and PC II, the correlation increased to 0.6 (Fig. 4). Thus, we conclude that, in summer, Clapper Rails were generally associated with dense vegetation ≥ 1 m in height, or with cattail-bulrush marshes <1 m tall.

Among the five transects with larger than expected densities of rails (Fig. 4), two (ranked 18 and 20 for PC I and PC II combined) were moderately dense cattail marshes. The remaining three transects included scattered trees mixed with cattail; two had relatively large amounts of loosestrife and associated vegetation, and two had relatively large amounts of grass.

Late summer-fall. In late summer and fall, densities of rails were significantly $(r_s = 0.441,$ P < 0.05) associated with tall, dense marsh vegetation. Rails were negatively associated with marshes with invading trees and grasses (PC III). This association was not significant $(r_s = 0.243)$, but when combined with PC I, the correlation was increased to $r_s = 0.615$ (Fig. 5). Five transects (those ranked 15, 16, 17, 20, and 21 on PC I and PC III combined) had substantially higher densities of rails than expected. Two (ranked 16 and 17) were moderately dense cattail areas. Another (ranked 15) was dense, but in addition to cattail, reed and loosestrife were also present. The last two (ranked 20 and 25) were sparse cattail-bulrush marshes with an intrusion of trees and grasses.



RANK OF PC I AND PC III

FIGURE 5. Correlations between ranks of Clapper Rail densities on transects with ranks of transects on the first and third principal components combined from the vegetation analysis during late summer-fall. Ranked densities arranged on vegetation ranks as in Figure 2.

Seasonal similarities in habitat use. The same transects were often high-use areas across seasons (Table 3). Independent of this finding, we noted that high use tended to be associated with relatively dense marshes with a height >2m. This led logically to the conclusion that marshes of high use across seasons were in fact denser and taller than average. To test this further, we averaged the PC I factor scores for transects that were ranked in the top six abundances in at least two seasons and for transects that never had rail density ranks in the top six abundances. This test revealed that transects that regularly had high density ranks had a significantly higher mean factor score on PC I than transects that never had high density ranks (Fig. 6).

Consistent deviations from the major trend *in habitat use.* Certain transects were found to consistently deviate from the expected rank of densities. In view of the consistency in direction of deviation, we decided to learn more about rail habitat use by studying these areas. Three transects had consistently higher densities of rails than predicted; one of them had a large proportion of reeds (Table 4) and the other two were rather sparse cattail marshes. The transect that consistently had fewer rails than expected was a dense cattail marsh not discernibly different in vegetation characteristics from marshes typically associated with many more rails. Physically, the marsh was smaller than average and had steep banks (Appendix 1).

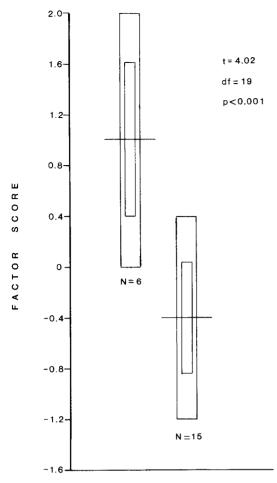


FIGURE 6. Mean factor score for transects that were ranked in the top six for Clapper Rail abundance in at least two seasons (left) and for transects that never had abundances in the top six ranks. Horizontal lines = \bar{x} . wide rectangle = 1 SD, and narrow rectangle = 2 SE.

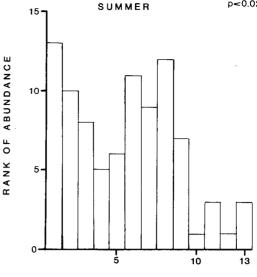
Effects of area size and bank slope. Size of an area was not a significant factor associated with density estimates (Table 5). Rail densities were just as likely to be high in smaller marshes as they were in larger marshes (Appendix 1). We further tested this by plotting the number of times that study areas 0-9.9 ha and ≥ 10 ha had above- and below-predicted ranks. Neither of the marsh size classes had more or fewer rails than expected with a frequency deviating significantly from that expected by chance.

We tested the possible effect of steep or gradual banks by tabulating the distribution of above- and below-expected ranks associated with marshes with steep vs. gradual banks. Bank slope was not significantly associated with predicted densities.

TEST OF HABITAT USE PREDICTIONS

Rail densities on 13 test transects correlated significantly with foliage density (PC I; Fig. 7).





RANK OF PC I

FIGURE 7. Correlations between rank of Clapper Rail densities on test transects with ranks of test transects on the first principal component of the vegetation analysis. Ranks of densities on vegetation ranks as in Figure 2.

More rails were present in marshes with relatively tall vegetation that consisted of either cattail, bulrush, or reed, or mixtures of these species. Rails were not consistently associated with marshes having grasses or trees distributed throughout. That the type of marsh vegetation present is not a major factor is implicit in this prediction. In the primary data set, there were no marshes dominated by bulrush. In the test set of transects, the densest marshes consisted of bulrush, and also had the most rails. The mean factor score on PC I for transects with the top five rail densities ($\bar{x} = 0.755$, SD = 1.21) and the mean for transects with the lowest five ranks ($\bar{x} = -0.745$, SD = 0.685) were significantly different (t = 3.4, 8 df, P < 0.02).

SEASONAL DENSITIES

During the breeding season, densities ranged from 0-8.0 birds/10 ha and averaged 2.5 (SD = 2.4) per 10 ha (Appendix 1). In winter, densities in marshes with rails ranged from 0.2 (SD = 0.2) to 2.8 birds/10 ha (SD = 3.5), but none was detected in 21 of the 27 marshes. Spring densities ranged from 0-6.2 birds/10 ha and averaged 1.1 (SD = 1.8) rails per 10 ha.

DISCUSSION

The Yuma Clapper Rail differs from all other known races of *Rallus longirostris* in that it inhabits freshwater in the breeding season but apparently winters in brackish marshes along

TABLE 4. Transects that consistently deviated from expected abundances of Clapper Rails across four seasons for
two years. Standard deviations in parentheses. $PC = principal component; DEN = foliage density; FHD = foliage height$
diversity; PI = patchiness index.

	Mean		Standardized score when deviation from expected densities			
Vegetation		Transects with top six	High			Low
variables	All transects	density ranks	IM-01	IM-04	1M-23	MA-04
PC I	0.010 (1.0)	1.220 (0.28)	-0.310	-0.812	-0.017	0.900
DEN 0.2 m	0.277 (0.15)	0.376 (0.16)	0.181	0.082	0.049	0.552
DEN 0.6 m	0.290 (0.18)	0.450 (0.09)	0.274	0.111	0.075	0.491
DEN 1.5 m	0.239 (0.18)	0.445 (0.08)	0.219	0.102	0.291	0.320
$DEN \ge 3.0 m$	0.053 (0.05)	0.128 (0.03)	0.031	0.006	0.058	0.081
Total DEN	0.859 (0.49)	1.399 (0.22)	0.705	0.304	0.474	1.444
FHD	0.592 (0.11)	0.668 (0.03)	0.650	0.652	0.525	0.610
PI	0.178 (0.25)	0.234 (0.09)	0.017	0.059	0.017	0.326
Cattail	0.406 (0.26)	0.384 (0.20)	0.400	0.387	0.000	0.434
Bulrush	0.037 (0.05)	0.055 (0.04)	0.000	0.072	0.000	0.050
Reed	0.091 (0.18)	0.177 (0.22)	0.000	0.000	0.617	0.054
Trees	0.119 (0.17)	0.011 (0.02)	0.022	0.010	0.000	0.033
Loosestrife	0.035 (0.06)	0.010 (0.02)	0.000	0.000	0.000	0.058
Grass	0.052 (0.08)	0.011 (0.03)	0.089	0.005	0.000	0.067

the western coast of Mexico (Banks and Tomlinson 1974). The race in central and southern Mexico, *R. l. tenuirostris*, is a permanent resident of freshwater; all other Clapper Rails use brackish habitats at all times.

The Yuma Clapper Rail is endangered because only a few thousand hectares of breeding habitat are available to it, much of which is threatened by human activities and natural vicissitudes. Although the construction of hydroelectric dams along the lower Colorado River has harmed much of the natural riparian habitat (Ohmart et al. 1977), these dams have apparently enlarged the total marsh habitat (Ohmart and Smith 1973, Ohmart et al. 1975). Yuma Clapper Rail populations have probably increased and the species has moved northward from the Colorado River Delta area in response to this increased amount of habitat. Although much of the habitat is within refuge boundaries (Fig. 1), that lying outside of protected areas is threatened by development. Habitat within refuges is subject to damage when prolonged extensive water releases from dams cause flooding and death of cattail. Such releases in 1983 and 1984 apparently caused a significant reduction in breeding success (R. Powell [Yuma Clapper Rail Recovery Team

 TABLE 5.
 Clapper Rail densities in marshes of various sizes.

Size of area (ha)	Number of	Number of Clapper Rails per 10 ha			
	marshes	Mean	SD		
0-4.9	11	1.89	2.50		
5.0-9.9	9	2.30	1.57		
10.0-14.9	6	3.90	2.86		
≥15	14	2.43	2.48		

leader, Blythe, CA], pers. comm.). Without corrective measures, a combination of habitat loss outside of refuges and greatly reduced breeding owing to sustained high water flows could severely cut the Yuma Clapper Rail populations.

Most of the habitat north of Mexico lies within the jurisdictional boundaries of the U.S. Bureau of Reclamation. Thus, their actions, or those of any other group working on federal lands, fall under the jurisdiction of U.S. wildlife protection laws. Our study provides data that should be helpful in identifying patches of habitat likely to be used by the Yuma Clapper Rail. These data should also be useful in designing habitat improvement projects.

Smith (1975) found in his study area, located at the northern edge of our study area (Topock Marsh), that Clapper Rails were most numerous in moderately dense cattail and bulrush marshes. Bennett and Ohmart (1978) found that at the Salton Sea (60 km west of our study area), rails preferred the densest cattail stands and did not use bulrush to any significant extent, possibly because bulrush marshes were frequently dry.

Clapper Rails eat mainly crayfish (*Procambarus* sp., *Oropectes* sp.) on the Colorado River north of Mexico (Ohmart and Tomlinson 1977). At Topock Marsh, crayfish are denser in moderately dense cattail than in dense cattail stands (Smith 1975). At the Salton Sea, however, crayfish are most abundant in dense stands of cattails (Bennett and Ohmart 1978).

Our analysis incorporated all of these findings. Data from nearly all of the species' total range on the lower Colorado River within the United States indicated that, although rails were primarily associated with dense vegetation, they regularly reached greatest densities in some cattail-bulrush marshes of only moderate foliage density. This finding suggests that perhaps crayfish usually reach greatest densities in dense vegetation, but at least some of the time they reach high numbers in less dense vegetation, as indicated by Smith's (1975) study at Topock Marsh. Our data demonstrate that Clapper Rails occur in vegetation other than cattail. This vegetation included dense reed and sparse cattail-bulrush stands where crayfish may have been fairly abundant.

From the analysis of data from 27 transects, we predicted that rails would be associated with dense vegetation and that plant species composition was not the critical feature. In the original set of transects, no marshes of dense bulrush were included. In the test set, the densest transects were bulrush. That the prediction held in the test set is a further indication that foliage density is an important attribute of Clapper Rail habitat.

All of the transects in our survey were on dikes or jetties or were within 15 m of land. Smith (1975) and Bennett and Ohmart (1978) presented data indicating that rails require high ground within the marsh. These investigators reported that, although adult rails can swim, the downy plumage of chicks quickly becomes matted when wet and they drown. The need for high ground in nesting habitat seems thoroughly documented, and we did not investigate the point further. Other comments concerning habitat requirements of Clapper Rails along the entire lower Colorado River, however, are based exclusively on the very local, but thoroughly quantified, data of Smith (1975) and Bennett and Ohmart (1978), or on highly subjective conclusions based on observations unsupported by any quantification of environmental variables (Tomlinson and Todd 1973, Gould 1975). Our purpose has been to address some of these comments and either substantiate or refute them on the basis of quantified data. Some conclusions were supported, others were not, and still others need further study.

Our major generalization is that rails seemed to prefer dense vegetation regardless of whether it was cattail or bulrush in all seasons and years. Cattail was by far the most abundant emergent marsh vegetation in the valley; most marshes had at least some cattail. Beyond that, however, neither cattail nor any other emergent vegetation was clearly associated with densities of Clapper Rail. A study of the exceptions revealed that rails were consistently associated with certain rather sparse emergents. Abundance of crayfish is probably a factor of major importance in these cases.

Smith (1975) stated that the size of a marsh

was important, with rails more abundant per unit area in larger marshes. We found marsh size to be independent of rail density per unit of area.

Smith (1975) also felt that steep banks adjacent to a marsh are a deterrent for Clapper Rails. This may be true but needs clarification. We have shown here that the negative feature is not the mere presence of a steep bank adjacent to the marsh. The birds require a dry interface between the banks and the water for walking and foraging. Where such an interface is lacking, the value of the marsh is probably reduced, but where it is even very narrow (25 cm), marsh quality probably is unaffected.

Low numbers of Clapper Rails were seen regularly throughout winter months. Habitat breadth is also narrower during winter, when crayfish are scarce, which fits with theories of optimal habitat use (e.g., Fretwell 1972).

Time was spent equally in all census areas in winter, but rails were found only in the southern part of the study area. Among the 14 locations inhabited by rails in spring (Appendix 1), 10 were near Imperial Dam at the southern end of the study area. Apparently, rails are basically migratory, with most birds leaving their summering grounds by the end of October and a small number remaining for the winter. In spring (March), returning Clapper Rails begin reaching southern portions of our study area (Imperial Dam).

Since this population of the Clapper Rail is classified as endangered, it is important to consider its total size in the lower Colorado River valley. We estimate the population in the 473 ha we studied as 119 birds. Knowing the total marsh area and assuming that our sample of marsh areas was representative of the marshes available for study, we can estimate the total rail population. Total emergent aquatic vegetation is estimated to be 2,361 ha along the Colorado River from Davis Dam to the Mexican border (Anderson and Ohmart 1976). Only stands of emergent aquatic vegetation were included in this conservative estimate; open water in marsh areas was excluded. For every hectare of emergent vegetation in the sample, there was roughly 1.25 ha of marsh when considering the proportion of open water. Multiplying 2,361 ha of emergents by 1.25 ha of marsh results in 2,951 total hectares of marsh. The population estimate for that part of the study involving 27 marsh areas yields an estimated 735 rails for the entire area north of Mexico. The test areas yield an estimate of 753 birds. This compares with 739 birds obtained by the Clapper Rail Recovery Team in 1973 and, after adjusting for some areas not censused, 690 birds for 1974 (Gould 1975). In the

past decade, the Recovery Team has consistently estimated between 700 and 800 birds (R. Powell, pers. comm.).

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(See Appendix 1, next page.)

APPENDIX 1. Individual transect location, and size and mean densities of Clapper Rails at four times of the year. Numbers in parentheses are 1 SD of the mean. The mean was calculated from the number present each month over three years.

	Transect location/		_	Mean density/10 ha				
	designation	Size (ha)	Slope of bank	Winter	Spring	Summer	Late summer-fall	
A.	Transects used to make predictions							
	32°49'N to 32°52'N IM-28	12.1	are duel	1 4 (1 4)	62(21)	5 4 (2 1)	25(20)	
	IM-28 IM-29	12.1	gradual gradual	1.4 (1.4) 0.4 (0.5)	6.2 (3.1) 2.2 (1.5)	5.4 (3.1) 4.9 (3.2)	3.5 (3.0) 2.6 (1.0)	
	IM-29 IM-31	6.0	gradual	2.8 (3.5)	5.9 (1.2)	2.8 (2.0)	3.4 (1.0)	
	IM-31 IM-23	6.0	gradual	0.2 (0.2)	1.1 (2.3)	0.7 (0.8)	0.3 (0.6)	
	IM-25 IM-21	6.0	gradual	0.2 (0.2)	3.9 (3.7)	1.8 (3.5)	0.8 (1.3)	
	IM-24	12.1	gradual	0.5 (0.8)	2.8 (4.8)	3.9 (2.7)	1.8 (0.5)	
	IM-25	12.1	gradual	0.2 (0.2)	2.1 (3.2)	0.2 (0.2)	5.4 (5.9)	
	33°08'N to 33°13'N							
	IM-01	3.0	gradual	0	0	8.6 (8.1)	2.3 (3.9)	
	IM-04	14.5	gradual	0	1.8 (2.2)	7.0 (8.6)	2.8 (3.9)	
	IM-09	7.8	gradual	0	1.3 (1.8)	4.4 (5.1)	0	
	IM-07	7.8	gradual	0	1.3 (2.0)	4.0 (3.9)	1.1 (1.5)	
	33°57'N to 34°00'N							
	MA-04	6.0	steep	0	0.8 (1.2)	2.8 (0.8)	0.6 (0.5)	
	MA-05	9.6	steep	0	0.7 (0.9)	3.5 (3.8)	1.8 (1.6)	
	MA-21	19.3	steep	0		1.0 (0.9)	0	
	MA-22	19.3	gradual	0	0.2 (0.4)	6.1(5.2)	0 0	
	MA-23	19.3	gradual	0	0	1.0 (1.7)	0	
	34°08'N to 34°18'N MA-24	19.3	staan	0	0	15(21)	0.7(1.2)	
	MA-24 MA-25	4.2	steep	0 0	0 0	1.5 (3.1) 0	0.7 (1.2) 0.3 (0.4)	
	MA-26	4.2	steep steep	0	0	0.4 (0.6)	1.1 (1.9)	
	MA-20 MA-27	3.0	steep	Ő	0	1.0 (1.7)	0.3 (0.4)	
	MA-28	3.0	steep	ŏ	ŏ	1.9 (1.9)	2.6 (2.3)	
	MA-29	1.8	steep	Õ	Õ	0	0	
	MA-30	1.8	steep	0	0	0	0	
	MA-31	9.6	steep	0	0	0.4 (0.6)	0.5 (0.9)	
	MA-32	9.6	steep	0	0	0.3 (0.8)	0	
	MA-33	3.0	steep	0	0	1.8 (1.9)	1.1 (1.9)	
	MA-34	3.0	steep	0	0	0.8 (1.0)	0	
	Total	242.7		_	_	_		
	Mean (SD)	9.0		0.2 (0.59)	1.13 (1.78)	2.49 (2.37)	1.22 (1.41)	
B.	Transects used to test predictions							
	32°49'N to 32°52'N							
	IM-32	13.6	gradual			6.8 (10.0)		
	33°57'N to 34°00'N							
	MA-01	29.4	gradual			3.1 (1.1)		
	MA-02	29.4	gradual			2.8(0.8)		
	MA-04 MA-05	2.4 3.8	gradual gradual			3.5 (3.8) 1.8 (1.2)		
		5.0	graduar			1.6 (1.2)		
	34°08'N to 34°18'N	257	-4			0.1 (0.1)		
	MA-06 MA-07	25.7	steep			0.1 (0.1)		
	MA-07 MA-08	$\begin{array}{c} 18.4 \\ 11.0 \end{array}$	steep steep			$\begin{array}{c} 0\\ 0\end{array}$		
	MA-09	29.4	steep			0		
	MA-10	18.4	steep			0.6 (0.5)		
	34°45′N					x y		
	TK-01	16.5	gradual			0.7 (1.2)		
	TK-02	17.7	gradual			8.0 (5.0)		
	TK-03	14.2	gradual			4.0 (4.4)		
	Total	229.9 •	c			_		
	Mean (SD)	18.5				2.55 (3.56)		
	Mean for 40 transects					2.51 (2.40)		