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# ENDANGERED LIGHT-FOOTED CLAPPER RAIL AFFECTS PARASITE COMMUNITY STRUCTURE IN COASTAL WETLANDS

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*Abstract*. An extinction necessarily affects community members that have obligate relationships with the extinct species. Indirect or cascading effects can lead to even broader changes at the community or ecosystem level. However, it is not clear whether generalist parasites should be affected by the extinction of one of their hosts. We tested the prediction that loss of a host species could affect the structure of a generalist parasite community by investigating the role of endangered Light-footed Clapper Rails (*Rallus longirostris levipes*) in structuring trematode communities in four tidal wetlands in southern California, USA (Carpinteria Salt Marsh, Mugu Lagoon) and Mexico (Estero de Punta Banda, Bahia Falsa–San Quintín). We used larval trematode parasites in first intermediate host snails (*Cerithidea californica*) as windows into the adult trematodes that parasitize Clapper Rails. Within and among wetlands, we found positive associations between Clapper Rails and four trematode species, particularly in the vegetated marsh habitat where Clapper Rails typically occur. This suggests that further loss of Clapper Rails is likely to affect the abundance of several competitively dominant trematode species in wetlands with California horn snails, with possible indirect effects on the trematode community and changes in the impacts of these parasites on fishes and invertebrates.

*Key words: California horn snail;* Cerithidea californica; *Clapper Rail; digenean trematodes; extinction; indirect effects; parasite;* Rallus longirostris levipes; *tidal wetland; trematode community*.

## INTRODUCTION

How does the extinction of one species affect the communities and ecosystems to which it once belonged? Direct impacts are certain if the extinct species has coevolved symbioses with other species (Temple 1977). Indirect effects may also result if the extinct species affected competitive interactions between other community members (Holt 1977) or drove trophic cascades (Estes et al. 1998). However, many species interactions are relatively subtle and the impacts of extinction or more localized extirpation may be difficult to detect. Some of the most ubiquitous, yet cryptic, members of communities are parasites and there is a growing body of evidence indicating that parasites can play important roles in both communities and ecosystems (Holt 1977, Price et al. 1988, Holt and Lawton 1994, Lindstrom et al. 1994, Lafferty and Morris 1996, Thomas et al. 1998, Lafferty et al. 2006). The fate of a parasite is intimately tied to that of its hosts (Stork and Lyal 1993, Windsor 1995, Koh et al. 2004). Although host extinction necessarily results in extinction of its specialist parasites, some parasites are generalists, using more than one host species. Here, we consider how the extinction of a single host from a complex host assemblage might affect a parasite community. To this end, we examine how the distribution and abundance of an endangered bird affects trematode parasite community composition in coastal wetlands.

The Light-footed Clapper Rail (*Rallus longirostris levipes*, Gruiformes: Rallidae) is a useful species for testing the hypothesis that host extinction can affect parasite community patterns. Clapper Rails are habitat specialists, occurring almost exclusively in vegetated portions of coastal wetlands. Tall stands of cordgrass (*Spartina foliosa*) and plants with similar structure (e.g., *Juncus* spp. and *Scirpus* spp.) are the preferred nesting and foraging habitat for Light-footed Clapper Rails; other wetland birds are typically absent or rare in this habitat. Furthermore, Clapper Rail populations are sedentary and adult birds are territorial, maintaining small home ranges throughout the year (Zembal et al. 1989). The numerical dominance, localized distribution, and long residence time of Clapper Rails in vegetated marsh habitat relative to other bird species suggest that Clapper Rails should disproportionately affect parasite communities in vegetated marsh. Finally, Light-footed Clapper Rails are declining or extirpated from much of their former range in California. Clapper Rail populations from wetlands in Baja California may also be declining (E. Palacios, *personal communcation*). Investigating parasite communities in wetlands with different

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Clapper Rail abundance permitted an examination of the impact of further loss of this state and federally endangered species.

Although directly quantifying the parasite communities of Clapper Rails is difficult for both practical and ethical reasons, digenean trematode parasites of Clapper Rails also use snail intermediate hosts that are relatively easy to sample. These trematode stages in snails provide a convenient "window" from which to view the trematode parasites of a local bird community (Huspeni and Lafferty 2004). The distribution and abundance of trematodes in snail populations is driven by the distribution and abundance of final host bird communities (Smith 2001, Hechinger and Lafferty 2005, Fredensborg et al. 2006). Adult trematode worms live in birds and the trematodes' eggs are deposited with the excreta of the final host birds. These eggs, or hatched trematode larvae, are infective to the snails. A well-studied guild of digenean trematodes parasitizes the California horn snail (*Cerithidea californica*; Martin 1972, Sousa 1983, 1993, Kuris 1990, Lafferty et al. 1994, 2006). Trematode infections in snails are long-lived and release free-swimming stages that encyst in or on second intermediate host fishes or invertebrates (Martin 1972, Kuris 1990, Huspeni and Lafferty 2004, Lafferty et al. 2006). Adult stages infect wetland birds (Pelecaniformes, Anseriformes, Gruiformes, Ciconiiformes, and Charadriformes). Birds, including Clapper Rails, become infected when they prey upon second intermediate host mollusks, crustaceans, polychaete worms, and fishes.

Adult trematodes in the California horn snail guild appear to be generalist parasites in final host birds (Russell 1960, Adams and Martin 1963, Didyk and Burt 1997). Due to the low host specificity of adult trematodes in this system, one might expect that the extinction of a single bird species would not strongly affect trematode communities. However, because wetland birds vary in diet, they differ in their frequency of exposure to trematodes that infect different types of second intermediate hosts (Martin 1972, Huspeni and Lafferty 2004, Lafferty et al. 2006). For instance, crabs and snails are important prey items for Clapper Rails (Jorgensen 1975, Heard 1982, Zembal and Fancher 1988, Eddleman and Conway 1998). Thus, we predict that Clapper Rails would be final host species to trematodes that use crabs and snails as second intermediate hosts. Furthermore, bird species also vary in their distribution among and within wetland habitats (Baker 1979, Burger et al. 1996, Long and Ralph 2001, Danufsky and Colwell 2003). Thus, heterogeneity in habitat use by birds, combined with variation in their trematode parasite fauna (due to dietary differences), might enable individual bird species to uniquely affect the spatial distribution of trematode infections in snails. We tested these predictions by examining whether the distribution of Clapper Rails influenced the community of trematodes in horn snails, particularly in the vegetated habitats where Clapper Rails live. Our findings support the idea that extinction of a single host species can significantly impact parasite community structure.

## Methods

### *Quantifying trematode infection in final host birds*

We used information on Clapper Rail diet and the use of second intermediate hosts by trematodes to determine those trematode species most likely to infect Clapper Rails. Clapper Rail diet information came from published accounts (Jorgensen 1975, Zembal and Fancher 1988, Eddleman and Conway 1998) and data obtained from dissecting two Clapper Rails found dead at Mugu Lagoon during the course of this study. Information on trematode second intermediate host use came from Martin (1972) and our familiarity with the system (Lafferty et al. 2006).

During the course of this study, we had the opportunity to dissect several specimens of wetland birds. This helped to confirm our assignment of Clapper Rail trematodes, and to assess the extent to which those trematodes also used other species of bird final hosts. To assess trematode parasitism in final host birds, we examined stomach and gut contents of wetland birds collected at Carpinteria Salt Marsh between February and July 2002 (CDFG Scientific Collecting Permit 803041, IACUC 2-01-594) and salvaged specimens supplied by the Santa Barbara Museum of Natural History (SBMNH) and the Environmental Division of Mugu Naval Air Weapons Station. Specimens collected at Carpinteria Salt Marsh included 11 species of shorebirds and two species of waterfowl. Two Clapper Rails were salvaged from Mugu Lagoon. Fresh specimens were kept on ice in the field and were dissected upon return to the laboratory using methodology developed by Doster and Goater (1997). We examined the digestive tract, hepatic portal system, kidneys, oviduct, and bursa of Fabricius (if present) of each specimen for adult digenean trematodes. Intestinal contents were sieved through 250-μm mesh to collect small trematode species. Trematodes were identified to species whenever possible, counted, fixed in AFA (Alcohal Formalin Acetic acid fixative), and preserved in 70% EtOH. Unidentified trematodes were stained and mounted for identification using available references (McDonald 1981, Schell 1985). We removed the stomach contents from each bird and preserved them in 90% EtOH. We later examined the stomach contents and identified all prey items.

### *Distribution of trematodes and Clapper Rails in Carpinteria Salt Marsh, Estero de Punta Banda, and Bahia Falsa*

We sampled one wetland in southern California from which Clapper Rails have been extirpated (Carpinteria Salt Marsh, CSM [34°24′5.75″ N, 119°32′13.4″ W]) and two wetlands in Baja California, Mexico with resident populations of Clapper Rails (Estero de Punta Banda,

EPB [31°46′29.8″ N, 116°36′42.0″ W] and Bahia Falsa, the west arm of Bahia San Quintín, BSQ [30°30′94.9″ N, 116°01′48.4″ W]). We used habitat-stratified random sampling to quantify trematode infection in horn snails. We also quantified final host bird abundance, distribution, and community composition in a 100 m radius circular plot centered on each snail sampling plot. We randomly selected 23 sampling plots in each wetland, stratified by habitat type (channel, vegetated marsh, mudflat, and pan), using ArcGIS 9.0 (ESRI 2004).

We quantified trematode communities in snails at each sampling plot. The minimum distance between snail sampling plots was 200 m, a distance exceeding the maximum home range size observed for Clapper Rails in California populations (Zembal et al. 1989). Snails were collected at EPB in fall 2002, at CSM in summer 2003, and at BSQ in summer 2004. In each sampling plot, we collected snails from 20 randomly placed 10 × 50 cm quadrats in a 10 × 10 m area. Because trematode prevalence varies with snail size (Sousa 1983, Kuris 1990), we restricted the size range of snails in our analysis to 25–29.9 mm (measured from the apex to the base of the shell). We attempted to collect 100 snails from each sampling plot. If fewer than 100 snails were collected using random sampling, additional snails were taken from within the sampling plot. Samples with fewer than 20 snails (five sampling plots at EPB, two at BSQ, and eight at CSM) were excluded from the analysis.

In each wetland, we obtained two estimates of Clapper Rail density. We conducted single high-tide, passive, visual censuses at EPB (2003) and BSQ (2004) in December to estimate Clapper Rail density in vegetated habitat within the sampling area for each wetland. Also, at each of the randomly selected sites where we sampled snails, we estimated local Clapper Rail abundance and distribution from data obtained during standardized surveys of final host birds conducted at each snail sampling plot. To sample birds, we conducted timed, passive, visual surveys while walking a 50 m radius circular transect in each bird-sampling plot. All birds detected in the sampling area were identified to species and were mapped onto an aerial photograph of the site. These data were entered into a spatial database for analysis. To quantify bird abundance and species composition at different tidal heights and to assess both the breeding and overwintering bird communities, we sampled each plot four times in summer (June–July) and six times in winter (December–January). Specifically, sampling at EPB was conducted between 26 June and 2 July and between 9 and 14 December 2003. At BSQ, we sampled birds between 23 and 28 June and between 5 and 10 December 2004. At CSM, we sampled birds between 17 June and 25 July 2004 and between 30 November 2004 and 22 January 2005.

To quantify Clapper Rail density adjacent to snail collection plots (local density), we generated a Clapper Rail abundance score from bird sampling data for each site. We weighted each Clapper Rail sighting so that birds with the highest scores were those observed in closest proximity to the snail collection plot. We then summed these weighted Clapper Rail observation data for each site to obtain the site-specific Clapper Rail abundance score (weighted Clapper Rail score for a site $= \Sigma[(n_1/x_1) + (n_2/x_2) \ldots + (n_n/x_n)]$ where $n$ is the number of Clapper Rails observed and $x$ is the distance of the Clapper Rails from the center of the sampling plot). Thus, high scores indicated greater Clapper Rail presence near the snail collection plot.

### *Trematode infection patterns in Clapper Rail territories at Mugu Lagoon*

To obtain an independent measure of the effect of Clapper Rails on parasite communities, we conducted an additional study of trematode parasites in Clapper Rail nest territories at Mugu Lagoon (MUGU), Ventura County, California (34°06′13.22″ N, 119°306′49.24″ W). At MUGU, we quantified trematode species' abundances in horn snails from six Clapper Rail territories and seven control plots. We selected Clapper Rail territories based on documentation of a Clapper Rail nest or territorial pair in 2003 and/or 2004 (M. Ruane, *personal commmunication*). Control plots were selected from adjacent areas of similar habitat with no documented observations of Clapper Rails between 1980 and 2004. We collected 100 horn snails (25–29.9 mm) within 20 m of each nest or control plot between September and December 2004.

### *Quantifying trematode infection in snails*

We examined the mantle and visceral mass of each snail for trematode sporocysts, rediae, or cercariae, identifying infections to species following Martin (1972) and T. C. Huspeni and R. F. Hechinger (*unpublished manuscript*). Immature infections were identified to the most specific taxonomic level possible and then were assigned to species in proportion to the relative abundance of the identified trematode species in each plot. We then calculated the prevalence (number of infections per number of snails dissected) of each trematode species for each sampling plot. Because post-recruitment competitive displacement of subordinate species occurs when more than one trematode species recruits in the same horn snail (Kuris and Lafferty 1994, Lafferty et al. 1994), we also calculated the "pre-interactive" prevalence of each trematode species, using the algorithm described in Lafferty et al. (1994). We used these estimates of trematode recruitment in parallel with all calculations and analyses performed using observed trematode prevalences.

We used two different metrics of trematode community structure to assess the importance of Clapper Rails to the larval trematode community in horn snails. In CSM, EPB, and BSQ, where we had estimates of Clapper Rail density at each site, we used trematode prevalence, a measure of trematode abundance that logically corresponds to Clapper Rail density. At

MUGU, we had only presence–absence data for Clapper Rails and therefore could not derive density estimates. To control for variation in the overall abundance of birds of all species, we quantified the proportion of Clapper Rail trematodes in the horn snail trematode community (number of Clapper Rail trematodes per total infections observed).

### *Analyses*

For all statistical analyses, we used parametric tests in JMP (SAS Institute 2004). We used primarily general linear models (GLMs), but also $t$ tests in our analyses. To determine an appropriate model for our analysis of CSM, EPB, and BSQ, we initially had to exclude CSM because the lack of Clapper Rails there would have made it impossible to assess interactions involving Clapper Rail abundance. We sequentially deleted all nonsignificant interactions ($P > 0.05$) and then included CSM in the model. After performing these analyses using pooled Clapper Rail trematode prevalence data, we performed analyses with each Clapper Rail trematode species as the response variable. We used sequential Bonferroni-corrected $P$ values (Rice 1989) to evaluate the results of these tests for individual trematode species. Assumptions regarding approximate normality and homogeneity of variance were assessed by inspecting normal quantile plots with Lillifors curves and plots of residuals vs. the predicted response variable (Quinn and Keough 2002). Response variable data were angular-transformed (Sokal and Rohlf 1981) when necessary to help meet model assumptions. We used ANOVA to examine distributional patterns of Clapper Rail trematodes among habitats and to test the effect of Clapper Rails on the proportion of Clapper Rail trematodes in snails from nest and control sites at MUGU. Because we had explicit, directional, a priori hypotheses regarding the effect of Clapper Rails on these trematodes in horn snails, those $P$ values are one-tailed and are indicated as such. All other $P$ values reported are two-tailed.

To explore the indirect effects of Clapper Rail extinction on non-Clapper Rail parasites, we estimated what the trematode community would look like at Mugu Lagoon if Clapper Rails went extinct. We first calculated the pre-interactive prevalence of all trematode species at the Clapper Rail nesting territories. We then simulated Clapper Rail extirpation by reducing the prevalence of the two trematode species that were significantly associated with rails (an undescribed *Himasthla* species and *Acanthoparyphium spinulosum*) to their estimated prevalences if rails were absent (determined by comparing rail to non-rail sites). We assumed that all double infections in our estimate would resolve in favor of the dominant trematode species. We then compared the prevalence of trematodes not significantly associated with rails, after the simulated extinction with the observed values (which were obtained by retaining the competitively dominant rail trematodes, but otherwise processed in the same manner, calculating pre-interactive prevalences and resolving double infections). This comparison yielded an estimate of the increase or decrease in prevalence of each trematode species that would occur if Clapper Rails were to be removed from those sites.

TABLE 1. Second intermediate hosts for trematode parasites that use *Cerithidea californica* as first intermediate host.

| Family and species | Primary second intermediate hosts |
|---|---|
| Clapper Rail-using species | |
| Echinostomatidae | |
| *Acanthoparyphium spinulosum* | snails, bivalves |
| *Himasthla rhigedana* | crabs, snails |
| *Himasthla* sp. B† | snails |
| Microphallidae | |
| *Probolocoryphe uca* | fiddler crabs |
| Notocotylidae | |
| *Catatropis johnstoni* | snails |
| Non-rail-using species | |
| Philophthalmidae | |
| *Cloacitrema michiganensis* | ghost and mud shrimp, bivalves |
| *Parorchis acanthus* | ghost and mud shrimp, bivalves |
| Cyathocotylidae | |
| *Mesostephanus appendiculatus* | fishes |
| Small cyathocotylid | fishes |
| Schistosomatidae | |
| *Austrobilharzia* sp. | none |
| Heterophyidae | |
| *Euhaplorchis californiensis* | fish |
| *Phocitremoides ovale* | fishes |
| *Pygidiopsoides spindalis* | fishes |
| *Stictodora hancocki* | fishes |
| Renicolidae | |
| Large xiphidiocercaria | polychaetes‡ |
| *Renicola buchanani* | fishes |
| *Renicola cerithidicola* | fishes |

*Notes:* For details on second intermediate host use, see Lafferty et al. (2006). Trematode species were classified as Clapper Rail trematodes if they used Clapper Rail prey as second intermediate hosts.

† Equals *Echinoparyphium* sp. of Martin (1972).

‡ R. F. Hechinger and J. R. Smith (*unpublished data*).

## RESULTS

### *Trematode infection in final host birds*

Five trematode species, *Catatropis johnstoni*, *Himasthla rhigedana*, an undescribed *Himasthla* species, *Acanthoparyphium spinulosum*, and *Probolocoryphe uca*, use Clapper Rail prey (either crabs [*Uca crenulata*, *Pachygrapsus crassipes*, and *Hemigrapsus oregonensis*] or California horn snails) as a second intermediate host. These were postulated to be "Clapper Rail trematodes" in our analyses. The remaining trematode species used second intermediate hosts that are not major components of Clapper Rail diets (Table 1). Our dissections of Light-footed Clapper Rails from Mugu Lagoon con-

TABLE 2. Effect of local Clapper Rail density (weighted abundance) on the prevalence of "Clapper Rail trematodes" in horn snails from all habitats at Carpinteria Salt Marsh, Estero de Punta Banda, and Bahia Falsa.

| Trematode and factor | $r^2$ | df | $F$ | $P$ |
|---|---|---|---|---|
| All Clapper Rail trematodes | | | | |
| Whole model | 0.75 | 6, 44 | 18.51 | <0.0001 |
| Wetland | | 2 | 19.84 | <0.0001 |
| Habitat | | 3 | 8.14 | 0.0003 |
| CLRA score | | 1 | 7.84 | 0.004† |
| *A. spinulosum* | | | | |
| Whole model | 0.62 | 6, 44 | 12.9 | <0.0001 |
| Wetland | | 2 | 1.96 | 0.156 |
| Habitat | | 3 | 7.05 | 0.0007 |
| CLRA score | | 1 | 35.87 | <0.0001† |
| *C. johnstoni* | | | | |
| Whole model | 0.16 | 6, 44 | 1.21 | 0.32 |
| Wetland | | 2 | 0.47 | 0.63 |
| Habitat | | 3 | 0.89 | 0.45 |
| CLRA score | | 1 | 0.89 | 0.18† |
| *H. rhigedana* | | | | |
| Whole model | 0.70 | 6, 44 | 14.47 | <0.0001 |
| Wetland | | 2 | 18.57 | 0.0002 |
| Habitat | | 3 | 3.56 | 0.0043 |
| CLRA score | | 1 | 11.59 | 0.0002† |
| *Himasthla* sp. | | | | |
| Whole model | 0.43 | 6, 44 | 4.72 | 0.001 |
| Wetland | | 2 | 3.76 | 0.03 |
| Habitat | | 3 | 5.91 | 0.002 |
| CLRA score | | 1 | 0.02 | 0.45† |
| *P. uca* | | | | |
| Whole model | 0.76 | 4, 44 | 8.66 | <0.0001 |
| Wetland | | 2 | 27.48 | <0.0002 |
| Habitat | | 3 | 7.13 | 0.0008 |
| Wetland × habitat | | 6 | 3.3 | 0.012 |
| CLRA score | | 1 | 0.1 | 0.38† |

*Notes:* The CLRA score is the site-specific Clapper Rail abundance score (weighted Clapper Rail score = $\Sigma[(n_1/x_1) + (n_2/x_2) \ldots + (n_n/x_n)]$, where $n$ is the number of Clapper Rails observed and $x$ is the distance of the Clapper Rails from the center of the sampling plot). High scores indicate greater Clapper Rail presence near the snail collection plot.

† One-tailed $P$ value for CLRA score.

firmed that at least two of these species, *H. rhigedana* and *P. uca*, occur as adults in Clapper Rails.

We also found three of the five postulated "Clapper Rail trematode" species in shorebirds and waders from CSM. We identified *A. spinulosum* from Black-bellied Plovers (*Pluvialis squatarola*) and Semipalmated Plovers (*Charadrius semipalmatus*) and *Himasthla* sp. in Short-billed Dowitchers (*Limnodromus scolopaceus*). Furthermore, we found horn snails (a second intermediate host for *A. spinulosum*, *H. rhigedana*, and *Himasthla* sp.) in the stomach contents of Short-billed Dowitchers and Western Sandpipers (*Calidris mauri*) and lined shore crabs (a second intermediate host species for *H. rhigedana*) in Willets (*Catoptrophorus semipalmatus*). This confirmed our expectation that our postulated "Clapper Rail trematodes" were not specific to Clapper Rails.

### *Clapper Rails*

We counted 99 Clapper Rails at EPB and six Clapper Rails at BSQ during the winter censuses of the sampling areas in these wetlands. We observed no Clapper Rails at CSM during either sampling or census efforts. With digitized habitat files, we calculated the area of vegetated habitat (pickleweed [*Salicornia* spp.] and cordgrass inclusive) in CSM, EPB, and BSQ to generate Clapper Rail density estimates. At EPB, we estimate that there were ~0.27 Clapper Rails/ha of vegetated marsh habitat and 0.07 rails/ha at BSQ. We detected 72 Clapper Rails during nontargeted sampling at EPB and BSQ. These Clapper Rails were detected in cordgrass-dominated vegetated marsh ($N = 58$) and cordgrass vegetation along channel edges (Whitney 2006).

### *Trematode infections in snails at Carpinteria Salt Marsh, Estero de Punta Banda, and Bahia Falsa*

Local Clapper Rail density (weighted Clapper Rail abundance), wetland, and habitat explained 75% of the variation in the prevalence of "Clapper Rail trematodes" in horn snails at CSM, EPB, and BSQ (Table 2). We found a significant and positive association between local Clapper Rail density and the prevalence of "Clapper Rail trematodes" in snails from sampling plots among habitats in these wetlands (Table 2). There were also significant effects of wetland and habitat on the prevalence of "Clapper Rail trematodes" in snails (Table 2). Among wetlands, the prevalence of "Clapper Rail trematodes" was greater in snails from vegetated marsh (the preferred habitat of Clapper Rails) and from mudflat than from either channels or pans ($r^2 = 0.23$, $F_{3,44} = 4.14$, $P = 0.01$).

Analyses using the individual trematode species as response variables and using the sequential Bonferroni-corrected $P$ values for multiple tests (Rice 1989) indicated that local Clapper Rail density was positively correlated with the prevalence of *A. spinulosum* and *H. rhigedana* among habitats in the three wetlands examined, but not with the other postulated "Clapper Rail trematode" species (Table 2). Wetland, habitat, or both significantly affected the prevalence of all of the Clapper Rail trematodes except *C. johnstoni* (Table 2). Prevalence of *H. rhigedana*, *Himasthla* sp., and *P. uca* varied significantly among wetlands. Prevalence of *H. rhigedana*, *Himasthla* sp., *P. uca*, and *A. spinulosum* differed significantly among habitats (Table 2). Analyses conducted using estimated "pre-interactive" prevalences of the five Clapper Rail trematode species gave results consistent with those obtained using observed prevalence data (Whitney 2006).

Using census data, we found a positive correlation between Clapper Rail density in vegetated marsh and the mean prevalence of "Clapper Rail trematodes" in horn snails from plots in vegetated marsh (Fig. 1). Using sequential Bonferroni-corrected $P$ values, we also found a positive correlation between Clapper Rail density in vegetated habitat and prevalence of *H. rhigedana* ($r^2 =$

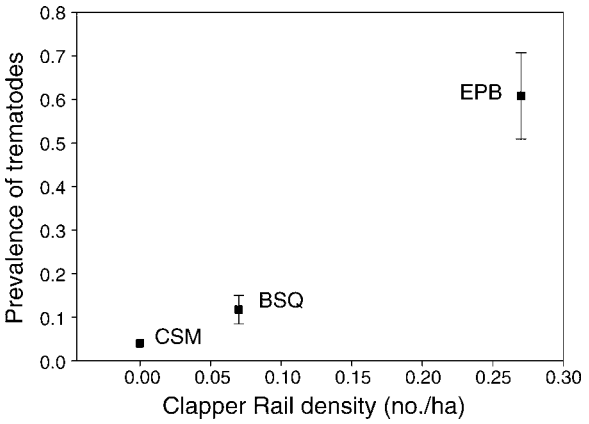


FIG. 1. The relationship between Clapper Rail density in vegetated habitat (estimates from census data) and the prevalence of Clapper Rail trematodes in horn snails from plots in vegetated marsh at Carpinteria Salt Marsh (CSM; $N = 1$), Bahia Falsa (BSQ; $N = 4$), and Estero de Punta Banda (EPB; $N = 3$) ($r^2 = 0.86$, $F_{1,7} = 37.04$, $P$ [one-tailed] = 0.0005). Values are means ± SE. Standard errors were calculated on angular-transformed data and then were back-transformed to prevalence values.

0.99, $F_{1,7} = 1324.80$, $P$ [one-tailed] = 0.009) and *P. uca* ($r^2 = 0.77$, $F_{1,7} = 19.81$, $P$ [one-tailed] = 0.002). We found no association between the estimated density of Clapper Rails in vegetated habitat and prevalence of *A. spinulosum* ($r^2 = 0.07$, $F_{1,7} = 0.08$, $P$ [one-tailed] = 0.41), *C. johnstoni* ($r^2 = 0.07$, $F_{1,7} = 0.08$, $P$ [one-tailed] = 0.42), or *Himasthla* sp. ($r^2 = 0.32$, $F_{1,7} = 0.48$, $P$ [one-tailed] = 0.31).

Using pooled data from vegetated marsh plots in all three wetlands, we found a positive correlation between local Clapper Rail density and prevalence of "Clapper Rail trematodes" among plots among the three wetlands (Fig. 2). Separate analyses of the five "Clapper Rail trematode" species using sequential Bonferroni-corrected $P$ values (Rice 1989) showed a positive and significant association between local Clapper Rail density and prevalence of *H. rhigedana* ($r^2 = 0.64$, $F_{1,7} = 10.79$, $P$ [one-tailed] = 0.01) in horn snails from vegetated plots. Prevalence of *A. spinulosum* was also significantly associated with local Clapper Rail density prior to correcting for the family-wide error rate ($r^2 = 0.50$, $F_{1,7} = 5.97$, $P$ [one-tailed] = 0.03). We found no significant associations between local Clapper Rail density and *P. uca* ($r^2 = 0.31$, $F_{1,7} = 2.7$, $P$ [one-tailed] = 0.08), *C. johnstoni* ($r^2 = 0.08$, $F_{1,7} = 0.53$), or *Himasthla* sp. ($r^2 = 0.10$, $F_{1,7} = 0.64$, $P$ [one-tailed] = 0.22) in horn snails from vegetated habitat.

### *Trematode infections in snails at Mugu Lagoon*

"Clapper Rail trematodes" composed more than twice the proportion of the trematode assemblage in infected snails from Clapper Rail nest territories than from control sites at MUGU (Fig. 3). Additional analyses using sequential Bonferroni-corrected $P$ values (Rice 1989) indicated that two of the five "Clapper Rail trematode" species, *Himasthla* sp. ($r^2 = 0.41$, $F_{1,12} = 7.79$, $P$ [one-tailed] = 0.009) and *A. spinulosum* ($r^2 = 0.38$, $F_{1,12} = 6.68$, $P$ [one-tailed] = 0.012), had significantly higher proportional abundance in infected snails from Clapper Rail nest territories than in snails from control sites. We found no association between Clapper Rails and the proportional abundance of either *C. johnstoni* ($r^2 = 0.20$, $F_{1,12} = 2.87$, $P$ [one-tailed] = 0.12), *P. uca* ($r^2 = 0.05$, $F_{1,12} = 0.59$, $P$ [one-tailed] = 0.23), or *H. rhigedana* ($r^2 = 0.004$, $F_{1,12} = 0.04$, $P$ [one-tailed] = 0.42) at Mugu Lagoon. Analyses conducted using estimated "pre-interactive" prevalences of trematodes in horn snails at Mugu Lagoon gave results consistent with those obtained using observed prevalence data (Whitney 2006).

### *Estimated indirect effects*

The simulated removal of Clapper Rails from nesting sites at MUGU resulted in an 87% decrease in prevalence of the "Clapper Rail trematodes," *Himasthla* sp. and *A. spinulosum*. The release from competition with these two competitively dominant "Clapper Rail trematodes" allowed a widespread (12/14) increase in the prevalence of "non-Clapper Rail trematode species" (range 0–33%, mean 13.6%). Of particular note, simulating Clapper Rail extirpation caused "non-rail trematodes" that parasitize fishes as second intermediate hosts to increase by 20.2%. These results only apply to a comparison of Clapper Rail territories, and effects would be more moderate at the scale of the entire marsh, where Clapper Rails would have a lower average influence.

## DISCUSSION

Although extinction of Clapper Rails would not result in the extinction of Clapper Rail trematodes, our results

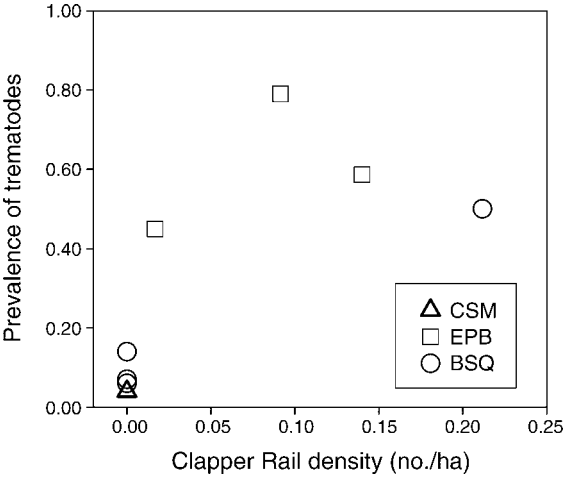


FIG. 2. The effect of local Clapper Rail density (weighted Clapper Rail abundance) on the prevalence of Clapper Rail trematodes in horn snails from vegetated marsh sites in Carpinteria Salt Marsh, Estero de Punta Banda, and Bahia Falsa ($r^2 = 0.50$, $F_{1,7} = 5.95$, $P$ [one-tailed] = 0.03).

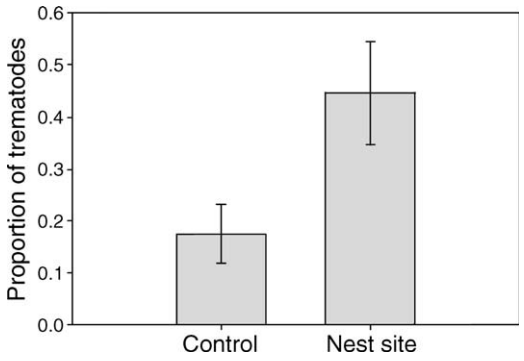


FIG. 3. The effect of Clapper Rails on the proportion of Clapper Rail trematodes (number of Clapper Rail trematodes/number of infected snails) in horn snails from nest territories ($N = 6$) and control plots ($N = 7$) at Mugu Lagoon ($t = 2.47$, $P$ [one-tailed] $= 0.015$). Values are means ± SE.

suggest that it would alter wetland trematode communities in significant ways. Despite the functional redundancy inherent in the final host guild, Clapper Rails were positively associated with the abundance of a subset of trematodes that parasitize the California horn snail in the wetlands that we examined. Consequently, extirpation of Clapper Rails could result in significant changes to wetland parasite communities, specifically to community composition of trematode parasites in horn snails living in vegetated marsh habitat. Although our results seem logical and are consistent with our predictions, we note that the study was necessarily based on observations (not experimental manipulations), such that unknown confounding variables could drive some of the patterns that we report.

The positive relationship between Clapper Rails and "Clapper Rail trematodes" was strongest in the vegetated habitat that this final host species preferentially occupies. Further, we consistently found the relationship both within and among wetlands. The overall pattern was largely a consequence of two trematode species, *H. rhigedana* (a species that used crabs and horn snails as a second intermediate host) and *P. uca* (which uses crabs as second intermediate hosts) being more abundant in habitats used by Clapper Rails. The "Clapper Rail trematode" species that do not use crabs as second intermediate hosts (*A. spinulosum*, *Himasthla* sp., and *C. johnstoni*) did not show a consistent pattern at the largest scale examined, namely, between wetlands. However, within wetlands, *A. spinulosum*, *H. rhigedana*, and *Himasthla* sp. were significantly associated with Clapper Rails, *C. johnstoni* was not, and the trematode *P. uca* varied significantly with Clapper Rail abundance in some wetlands but not in others. Finally, at Mugu Lagoon where we controlled for the effect of habitat, *A. spinulosum* and *Himasthla* sp. were significantly associated with Clapper Rail nesting territories.

Although the trends that we found were consistent when we pooled all Clapper Rail trematodes, the trematode species individually were not always associated with Clapper Rails at the scales that we examined. In particular, the putative "Clapper Rail trematode" *C. johnstoni*, was never associated with Clapper Rail abundance in our study. This may have been due to its relatively low prevalence in the wetlands that we examined, or it may be that Clapper Rails are not important hosts for this species. The inconsistencies in association with Clapper Rails among the other trematode species could be explained by two factors. The observed patterns could reflect variation in the distribution of second intermediate host species among wetlands, affecting the relative abundance of these prey items in Clapper Rail diets. They could also result from differences in bird communities among these wetlands, altering the extent to which other final host species affect the distribution of trematodes species common to Clapper Rails.

Habitat consistently affected the abundance of "Clapper Rail trematodes" in our large-scale study. Because other species of wetland birds can serve as hosts for the trematode species that infect Clapper Rails, it is not surprising that the associations between Clapper Rails and abundance of "Clapper Rail trematodes" were most apparent within the vegetated areas in the marsh, the preferred habitat of Clapper Rails. Abundance of these same trematodes in horn snails on mudflats, open habitat avoided by the secretive Clapper Rails, is due to the presence of other final host species, notably shorebirds that are numerous on mudflats. It is reasonable to conclude that Clapper Rails do not contribute significantly to community structure in habitats that they do not use. However, it appears that the effect of Clapper Rail abundance was strong enough to drive their positive association with the prevalence of "Clapper Rail trematodes" in horn snails across all wetlands examined because most of the area of these marshes was vegetated. In support, we also observed the association of Clapper Rails and "Clapper Rail trematodes" in Mugu Lagoon where we were able to control for the effect of habitat.

We cannot conclude that the extinction of Clapper Rails will affect parasite communities in all coastal wetlands. For instance, at CSM, where Clapper Rails are now extirpated, California horn snails are relatively rare in vegetated marsh habitat (perhaps because vegetation is uniformly dense in this marsh). For this reason, we would expect that Clapper Rails at CSM had less overlap with host snails in comparison to the present situation at EPB and BSQ. In addition, Clapper Rails are also extant in some wetland systems where California horn snails do not occur. Because snails are necessary for completion of trematode life cycles, the significance of our results is limited to those locations where horn snails and Clapper Rails overlap in habitat use.

In general, there is a relationship between final host birds and trematode abundance in this system. In

particular, the abundance and diversity of bird communities drives the abundance and diversity of trematode communities in snails (Hechinger and Lafferty 2005). This suggests a pattern at a broader scale than we have described for Clapper Rails. Just as impacts to a single host species, such as the Clapper Rail, may result in changes in the abundance or distribution of some trematode species, impacts to wetland bird communities should affect trematode communities and lead to decreases in trematodes in general. Trematode communities appear to reflect the local abundance and diversity of final host communities; hence, these parasites are positive indicators of the integrity of coastal wetlands (Huspeni et al. 2005). In support of this contention, trematode prevalence and species richness increased following wetland habitat restoration, presumably because restored areas supported more birds (Huspeni and Lafferty 2004).

Changes in the abundance of "Clapper Rail trematodes" could affect the abundance of other trematode species. Larval trematodes compete vigorously for resources in the first intermediate host and competitively dominant species routinely prey upon and displace subordinate species from individual snails (Kuris 1973, Lie 1973, Lie et al. 1973, Combes 1982, Sousa 1992). This decreases the prevalence of subordinate trematode species (Kuris and Lafferty 1994). Three of the four trematode species that were significantly associated with Clapper Rail density, *A. spinulosum*, *H. rhigedana*, and *Himasthla* sp., are strong, competitively dominant species (Sousa 1993). Reduced abundance of these dominant species would open up competitor-free space for subordinate species, enhancing their recruitment opportunities. For instance, our results suggest that other trematode species would increase in prevalence by an average of 13% if Clapper Rails were extirpated from a breeding territory. Furthermore, such changes to trematode communities in California horn snails could have consequences for other hosts in the life cycle. For instance, one of the trematode species that would be predicted to increase following the loss of the competitively dominant "Clapper Rail trematodes" (we estimated that it would increase 20% at MUGU Clapper Rail territories) infects killifish as a second intermediate host and greatly increases their susceptibility to predation by piscivorous birds (Lafferty and Morris 1996).

In conclusion, extinction of a single host species can affect the community of generalist parasites. Extirpation of Clapper Rails could affect parasite community structure in wetlands throughout the range of California horn snails. Although the fate of generalist parasites, such as trematodes in birds, is not exclusively tied to the fate of specific hosts, our findings indicate that loss of Clapper Rails from locations where horn snails are present would probably be associated with declines in certain species of trematodes. This could indirectly trigger an increase in populations of those trematode species with which the competitively dominant "Clapper Rail trematode" species compete. Our findings suggest that the magnitude of these effects within a wetland will increase with the extent of vegetated habitat and the degree to which the wetland supports California horn snails. As vegetated marsh typically comprises a large percentage of total habitat in coastal wetlands of southern California and Baja California Mexico (50.2% at EPB, 56.7% at BSQ, and 70.8% at CSM), changes in trematode communities in horn snails resulting from extirpation of Clapper Rails could affect a large proportion of the trematodes in these ecosystems.

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