California Fish and Game 102(4):157-161; 2016

Environmental extremes and biotic interactions facilitate depredation of endangered California Ridgway's rail in a San Francisco Bay tidal marsh

Cory Overton*, Steven Bobzien, and Marcia Grefsrud

U.S. Geological Survey, Western Ecological Research Center, Biological Research Division; Dixon Field Office, 800 Business Park Drive, Dixon, CA 95620, USA (CO)

East Bay Regional Park District; 2950 Peralta Oaks Ct, Oakland, CA 94605, USA (SB)
California Department of Fish and Wildlife; 1416 9th Street, 12th Floor, Sacramento, CA 95814, USA (MG)

**Correspondent: coverton@usgs.gov*

Key words: apparent competition, *Falco peregrinus*, high tide, peregrine falcon, predation, *Rallus obsoletus obsoletus*, Ridgway's rail, San Francisco Bay, tidal marsh

---

On 23 December 2015 while performing a high tide population survey for endangered Ridgway's rails (*Rallus obsoletus obsoletus*; formerly known as the California clapper rail) and other rail species at Arrowhead Marsh, Martin Luther King Jr. Regional Shoreline, Oakland, California, the authors observed a series of species interactions resulting in the predation of a Ridgway's rail by an adult female peregrine falcon (*Falco peregrinus*). High tide surveys are performed during the highest tides of the year when tidal marsh vegetation at Arrowhead Marsh becomes inundated, concentrating the tidal marsh obligate species into the limited area of emergent vegetation remaining as refuge cover. Annual mean tide level (elevation referenced relative to mean lower low water) at Arrowhead Marsh is 1.10 m, mean higher high water is 2.04 m (NOAA National Ocean Service 2014) and the average elevation of the marsh surface is 1.60 m (Overton et al. 2014). Tidal conditions on the day of the survey were predicted to be 2.42 m. Observed tides at the nearby Alameda Island tide gauge were 8 cm higher than predicted due to a regional low-pressure system and warmer than average sea surface temperatures (NOAA National Ocean Service 2014). The approximately 80 cm deep inundation of the marsh plain was sufficient to completely submerge tidal marsh vegetation and effectively remove 90% of refugia habitats.

At approximately 0945 hours, about 15 minutes into the survey, a moderate (12-20) flock of diving ducks, mostly lesser scaup (*Aythya affinis*), and a mixed flock of shorebirds consisting of least sandpipers (*Calidris minutilla*), western sandpipers (*Calidris mauri*), and willets (*Catoptrophorus semipalmatus*) were observed from approximately 200-250 m away swarming in low flight over the water. The behavior was classic predator avoidance flocking as the birds were being cooperatively hunted by a pair of adult peregrine falcons. The relative size difference between the falcons' size indicated a male (smaller)

and female (larger) pair (Figure 1). The male falcon initially appeared to be in pursuit of the shorebirds and would exhibit relatively low and level flight causing the swarming behavior near the water surface. Meanwhile, the female falcon performed several shallow stoops into the flock of diving ducks. Approximately three unsuccessful falcon attacks in rapid succession were observed. During the last failed attack, swarming by the diving ducks disturbed a Ridgway's rail that was hiding in what little hybrid cordgrass (*Spartina* spp.) remained above the tide. The rail made a low and short flight of approximately 1 m and then returned to the water (Figure 2). Suddenly, the falcons abandoned their pursuit of the shorebirds and diving ducks and began relentlessly stooping at the swimming rail. The first approximately six attacks were avoided by the rail which briefly dived under water or was simply missed by the two falcons. On a subsequent pass, the female falcon was able to capture the rail from the water surface and carry it into the air (Figure 3). Within seconds, several immature and mature western gulls (*Larus occidentalis*) mobbed the female falcon carrying the rail (Figure 4). As the pair of falcons flew out of visual range, the male aggressively engaged and drove away the gulls. The male falcon did this by flying above and behind the female and diving at any gull that approached within 5 to 10 m of the female. Two or three diving maneuvers by the male successfully deterred pursuit by the gulls.

These observations provide evidence of several important species interactions in San Francisco Bay tidal marshes, as well as environmental conditions that drive some of these interactions. First, the cooperative hunting behavior of peregrine falcons clearly suggests that

Figure 1. —A pair of peregrines after the successful cooperative capture of a Ridgway's rail. The female was identified as the larger of the falcons and carried the rail away with the smaller male following behind. Photo credit: Marcia Grefsrud/CDFW.

Figure 2. —Ridgway's rail flushing from sparse, flooded Spartina at Arrowhead Marsh, Oakland, CA. During the highest tides, available cover for concealment is reduced and individuals concentrate in the little exposed vegetation that remains. Photo credit: Marcia Grefsrud/CDFW.

Figure 3. —A female peregrine falcon's successful capture and flight with the Ridgway's rail. Photo credit: Marcia Grefsrud/CDFW.

Figure 4. —Western gulls chasing the female peregrine falcon as she carries a captured Ridgway's rail away. Photo credit: Marcia Grefsrud/CDFW.

pair-bonded individuals (mated pairs) benefit from an intraspecific mutualism that advantages each member of the pair through increased capture success, decreased energy used defending successful kills due to safeguarding by mates, decreased prey loss due to kleptoparasitism, and increased provisioning from food sharing. Cooperative hunting is uncommon in birds but has been observed, with some of the above benefits, in Aplomado falcons (*Falco femoralis*), (Hector 1986). A second biological interaction of importance is the rapid opportunistic prey switching behavior that occurred following the exposure of the Ridgway's rail. The hunting time and energy expended by the peregrine falcon pair to capture and kill the rail was likely much lower than the effort expended in their continued air to air pursuit and unsuccessful attacks on the diving ducks and shorebirds. While the ducks and shorebirds relied on swarming behavior, presence of conspecifics, and speed to evade the falcons, the rail appeared to initially depend on concealment to avoid detection. The effectiveness of relying on a concealment strategy decreases substantially in San Francisco Bay during the winter when extreme high tides correspond with winter storm events and low pressure systems (NOAA National Ocean Service 2014, Overton et al. 2014). These high tides are typically the most extreme of the year and occur during daylight (noting that summertime high tides may be of near equal height but occur at night). The combination of diurnal high tides and relatively homogenous vegetative cover results in a rapid decrease in suitable refuge habitat, and increases rail exposure to raptor predation events during these winter high tides (Figure 2). In addition, the presence of shorebirds and diving ducks, many species of which reach greatest abundance during the winter (Page et al. 1999), that flock together over the marsh plain prior to the falcons' arrival may serve as a source of apparent competition (Holt 1977) that indirectly reduce the likelihood of the rail surviving. The flocks of massed shorebirds and diving ducks were the initial targets of the falcons, as well as the apparent source of the disturbance that flushed the concealed rail from sparse cover, ultimately resulting in its depredation. Although this does not prove apparent competition, as it is possible that falcons would intensively hunt inundated tidal marshlands that contain the secretive rail even without

the much more visible shorebirds and waterfowl being present, it is apparent in this case that the survival of the rail was negatively influenced by the presence of such alternative prey for the falcon. Other sensitive species in San Francisco Bay, such as California least tern (*Sterna antillarum browni*) and snowy plover (*Charadrius nivosus*), have been preyed upon by peregrine falcons and may be similarly affected by indirect biotic interactions.

Although these types of interactions may result from environmental conditions (i.e., extremely high tides) that exist for just a few hours per year in the San Francisco Bay, the fragmented and diminished condition of tidal marsh habitats, together with sea level rise, cumulatively increase the risks to rail populations by reducing the extent of suitable transition vegetation communities between intertidal and upland ecotones.

Concerns are heightened given the limited number of Ridgway's rails, its relatively poor escape capability, and its vulnerability to extant hazardous environmental conditions. Loss of this transition zone habitat may limit the ability of rails to find refuge and escape predation from avian predators (Casazza et al. 2016).

Acknowledgments

We thank Joshua Hull, Elliot Matchett, Mike Casazza, and two anonymous reviewers who provided helpful comments and greatly improved the quality of this manuscript.

Literature cited

Casazza, M. L., C. T. Overton, T-V. D. Bui, J. M. Hull, J. D. Albertson, V. K. Bloom, S. Bobzien, J. McBroom, M. Latta, P. Olofson, T. M. Rohmer, S. Schwarzbach, D. R. Strong, E. Grijalva, J. K. Wood, S. M. Skalos, and J. Takekawa. 2016. Endangered species management and ecosystem restoration: finding the common ground. Ecology and Society 21(1):19. doi: 10.5751/ES-08134-210119

Hector, D. P. 1986. Cooperative hunting and its relationship to foraging success and prey size in an avian predator. Ethology 73(3): 247-257. doi: /10.1111/j.1439-0310.1986.tb00915.x/full

Holt, R. D. 1977. Predation, apparent competition and the structure of prey communities. Theoretical Population Biology 12(2):197-229.

NOAA National Ocean Service. 2014. San Leandro Channel, San Leandro Bay, CA StationID: 9414724 [Internet]. Tides and Currents; [cited 15 April 2014]. Available from: https://tidesandcurrents.noaa.gov

Overton, C. T., M. L. Casazza, J. Y. Takekawa, D. R. Strong, and M. Holyoak. 2014. Tidal and seasonal effects on survival of the endangered California clapper rail: does invasive Spartina facilitate greater survival in a dynamic environment? Biological Invasions 16(9): 1897-1914. doi: 10.1007/s10530-013-0634-5

Page, G. W., L. E. Stenzel, and J. E. Kjelmyr. 1999. Overview of shorebird abundance and distribution in wetlands of the Pacific Coast of the contiguous United States. The Condor 101(3): 461-471.

Submitted 01 November 2016
Accepted 13 January 2017
Associate Editor was N. Clipperton