

Assessing ecological interaction of California black rail (*Laterallus jamaicensis coturniculus*) and Virginia rail (*Rallus limicola*) using stable isotope analysis

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Abstract The California black rail (*Laterallus jamaicensis coturniculus*) and Virginia rail (*Rallus limicola*) are cryptic species of marsh birds that often coexist in the same wetland sites. The black rail is currently listed as threatened in California. Little is known about the diet of either bird species and their interactions due to their secretive nature. It has been suggested that black and Virginia rails compete for food sources since they occupy similar habitats. I used stable isotope analysis of carbon and nitrogen of the rail feathers to examine the diet and trophic level of the rails to determine whether the two rail species compete or partition resources. The results showed that there is no significant difference in the carbon and nitrogen isotope signature between black and Virginia rail feathers from the foothills population but a significant difference in carbon and nitrogen isotope signature between black and Virginia rails from the San Francisco Bay. This suggests that the two rail species in the foothills compete for food sources while the two rail species in the San Francisco bay partition food sources.

Introduction

The black rail (*Laterallus jamaicensis*) is one of the few birds that remain poorly understood since its discovery in 1760 (Allen 1900). The black rail is the smallest rail in North America and little is known about its life history, diet, distribution, and abundance due to its secretive nature (Wilbur 1974, Flores and Eddleman 1995). The black rail is currently listed as threatened in the state of California, primarily due to a rapid loss of its wetland habitat as a result of anthropogenic activities (Evens *et al.* 1991, Richmond *et al.* 2008).

Historically, the western subspecies of black rail, California black rail (*Laterallus jamaicensis contorniculus*) was first thought to be limited to the Southern California coastal region, the San Francisco Bay-Delta estuary, Morro Bay (San Luis Obispo County), and the outer coastal marshes at Tomales Bay (Marin County) (Wilbur 1974, Evens *et al.* 1991). In 1969, the first inland population of black rail was documented along the lower Colorado River in Arizona (Snider 1969). In 1994, another previously unknown population of black rails was discovered in the foothills of the Sierra Nevada Mountains, near Marysville, California (Aniger *et al.* 1995, Richmond *et al.* 2008). Although there have been several studies done on the Southern California and San Francisco Bay black rail populations (e.g. Evens *et al.* 1991, Flores and Eddleman 1995), little is known about the recently discovered population in the Sacramento Valley and Sierra Nevada foothills.

The black rail is an interesting species for the field of avian conservation because there is still much to learn about the life history, food preferences, and population dynamics (Eddleman *et al.* 1994). Current conservation efforts for black rails have focused on preserving wetland habitats and improving wetland management through investigating wetland habitat usage by the black rail (Flores and Eddleman 1995, Conway and Sulzman 2007). There are few comprehensive studies (e.g. Weske 1969, Flores and Eddleman 1991) that looked at the diet of black rails. Comparing different populations of black rail, with regard to their food preferences and potential competitors, will allow a better understanding of black rail ecology, leading to more effective conservation practices.

Although the Virginia rail (*Rallus limicola*) often coexists with the California black rail in the wetlands of Sierra Nevada foothills, little is known about the interaction between the two species (Beissinger *et al.* 2008). Within the Sierra Nevada foothills, both Virginia and California black rails inhabit patches of emergent wetlands. According to the U.S. Fish and Wildlife Service

(USFWS) classification system, the wetlands found in the region are characterized as palustrine persistent emergent wetlands (Cowardin *et al.* 1979), which are inland wetlands dominated by vegetation that remains standing year round until the next growing season. This wetland is typically characterized by cattails (*Typha* spp.), bulrushes (*Scirpus* spp.), reeds (*Phragmites australis*), sedges (*Carex* spp.), and smartweeds (*Polygonum* spp.).

The California black rails are highly habitat-specific and are generally found in both freshwater and saltwater marshes that are gently sloped, contain dense vegetation cover, and have shallow water (< 3 cm) with minimal water fluctuations (Eddleman 1994, Flores and Eddleman 1995, Richmond *et al.* 2008). Also, the black rails prefer wetlands sites with dense vegetation cover and moist to muddy substrate. The California black rail possesses a short tarsus length with an average 21.1 mm for males and 20.8 mm for females (Eddleman *et al.* 1994). The habitat structures preferred by the black rails can be explained by their short tarsal length, where it has been recorded in shorebirds that birds with shorter legs utilize habitat that has shallow water (Sayre and Rundle 1984).

The Virginia rails are found in similar habitat as the California black rails, such as wetland sites with shallow water, emergent vegetation cover, and moist to muddy substrates (Conway 1995, Taylor and Perlo 1998). One main difference is that the Virginia rails are found to occupy wetland site with greater water depth than black rails. This may be because the Virginia rail have longer tarsus length with average 41.4 mm for male and 38.2 mm for females (Taylor and Perlo 1998). On average, the Virginia rail use wetland sites with shallow water up to 15 cm, but it has been documented that Virginia rails use areas where water rises up to 27 cm deep (Taylor and Perlo 1998). Given that both black and Virginia rail often inhabits similar ecosystem, it is unclear why only the black rail population is threatened while the Virginia rail population remained unaffected. Information on the diet of the rail may help to understand this phenomenon.

It has been suggested that the Virginia rail may be a potential competitor to the black rail for food sources in the wetland, since the interaction between the two rail species is not well understood (Beissinger *et al.* 2008). Current knowledge on the diet of the two rail species is limited to predictions based on the morphological characteristics of the rails, while only a few studies have actually documented the stomach contents of black (e.g. Flores and Eddleman 1991, Eddleman *et al.* 1994) and Virginia rails (e.g. Horak 1970, Pospichal 1952). The bill shape of

black rail suggests a generalized feeding style, such as pecking at individual food items or gleaning over water or substrate to feed. The Virginia rail has a long shaped bill that feeds mainly by probing its bill into mud, shallow water, and under floating or matted vegetation (Conway 1995). The study by Flores and Eddleman (1991) recorded the stomach content of seven black rails that resulted from trap mortality between 1986 and 1988. A study by Hoark (1970) documented stomach content of 37 Virginia rail collected from direct shooting and trapping. However, no previous studies have examined the interaction between black and Virginia rails in regards to diet, while the existing studies on the stomach content do not provide sufficient information to determine whether black and Virginia rail partition or compete for food sources due to a small number of black rails sampled (e.g. Weske 1969, Flores and Eddleman 1991).

the limited documentation of the stomach content for both rail species provides little clarification on whether black and Virginia rails partition or compete for food sources.

Both the black and Virginia rail are secretive species, making it difficult to use typical techniques for studying bird diet choices, such as mark-recapture or field observation. The dense vegetation cover of their habitat renders direct observation impractical, while satellite telemetry is also ineffective, since it is only suitable for birds weighing at least 600 grams, while both rail species weigh less than 200 grams (Flores and Eddleman 1995, Webster *et al.* 2002). While radio telemetry with light weight transmitters may offer information on habitat usage by the rails, this does not necessarily reflect the food choices of the black and Virginia rails, and is of little help for studies of their diets. In addition, radio transmitters may hinder the movement of the animal and have a negative impact on field study (Hobson and Wassenaar 2008).

Stable isotope analysis of animal tissues has been widely used for understanding the food web structure of ecosystems and to track food sources of animals (Thompson and Furness 1995, Newsome *et al.* 2007, Hobson and Wassenaar 2008). Isotope signatures of food sources are unique from one another and are deposited into feathers once they are grown (Mizutani *et al.* 1992, Kelley and Finch 1998). The isotope signatures of the food items remain inert in the feathers until processing for stable isotope analysis. Stable isotope analysis offers great advantages to inferring the diet of black and Virginia rails compared to other methods. The rails only need to be captured once to collect feather samples to be used for analysis to infer the diet of the rails. More importantly, this is a nondestructive method to study food choices, and is

especially useful for species protected by law such as the California black rail (Thompson and Furness 1995).

Stable isotope analyses has been widely used in ecological studies (Peterson and Fry 1987, Hobson and Wassenaar 2008). The basis of stable isotope technique is that many elements have heavy and/or light isotopes that occur naturally in the environment (Hoefs 2004). The atoms of these elements with isotopes contain the same number of proton and electrons, but differ in the number of neutrons (Fry 2006). The variation in the number of neutrons of the same element results in difference in the molecular weight of the isotope. Stable isotope values are often expressed as the ratio of the heavy to light isotope and converted to delta (δ) notation. The sample isotope ratio is measured relative to isotope ratio of internationally accepted standard (Hobson and Clark 1992, Hobson and Wassenaar 2008). Common standards for carbon include PeeDee Belemnite (PDB) and Vienna-PDB (VPDB), and the standard for nitrogen isotope is atmospheric air (AIR) (Fry 2006, Hobson and Wassenaar 2008).

Of all the elements with multiple isotopes, carbon, hydrogen, nitrogen, oxygen, and sulfur are elements that are of most use in ecological studies (Hobson and Wassenaar 2008). Furthermore, carbon and nitrogen isotopes can be especially useful for identifying the habitat or trophic level of the study organism and food items consumed by animals that are difficult to observe. Carbon isotope analysis is useful in distinguishing between freshwater and marine habitat where the study organism feeds (Hobson and Wassenaar 2008). Also, stable carbon isotope analysis can identify different categories of plants based on the different photosynthetic pathways of the plant use, such as the C₃, C₄, and CAM plants (Newsome *et al.* 2007, Hobson and Wassenaar 2008). Nitrogen isotope analysis can help identify the trophic relation of the study organism and its food source (Peterson and Fry 1987, Vanderklift and Ponsard 2003). Typically for every trophic level, carbon isotopic value becomes enriched between 0.0 to 1.0‰ and nitrogen isotopic value increase by 3 to 5‰ (Peterson and Fry 1987).

The diet preference is unclear among different population of black rails and between black and Virginia rail. I used stable isotope analysis from feather samples collected from rails in Sierra Nevada foothills and San Francisco Bay area to understand the food choices of two different black rail populations and diet between black and Virginia rail. The objectives of my study are to 1) examine the ecological interaction of black and Virginia rail by observing diet preferences of the two rail species from Sierra Nevada foothills and San Francisco Bay using

isotope signatures obtained from the feathers, and 2) the diet preferences of black rail population from Sierra Nevada foothills and San Francisco Bay region. I hypothesize that there is no significant difference for the isotope signatures of carbon and nitrogen between black and Virginia rail even when considering regional differences. I also hypothesize that there is no significant difference between the carbon and nitrogen signatures for the black rail population from Sierra Nevada foothills and San Francisco Bay.

Methods

Feather Collection Feather samples were collected from the inland population of California black and Virginia rails from Butte, Nevada, and Yuba Counties, California, in the region known as the Sierra Nevada foothills. We collected breast feathers from all the captured rails, as well as back and tail feathers from several of the rails captured. All the feathers from the foothill were collected between July-August during 2004, 2007, and 2008. We used mist nets and drop-door traps with drift fences at eight different wetland sites, capturing a total of thirteen California black rails and five Virginia rails. Once the rails were captured, we banded the rails with individually numbered standard U.S. Geological Survey (USGS) aluminum leg bands. The wetland study sites were selected by satellite imagery and field surveys conducted by the Beissinger Lab in previous years (1994-2008).

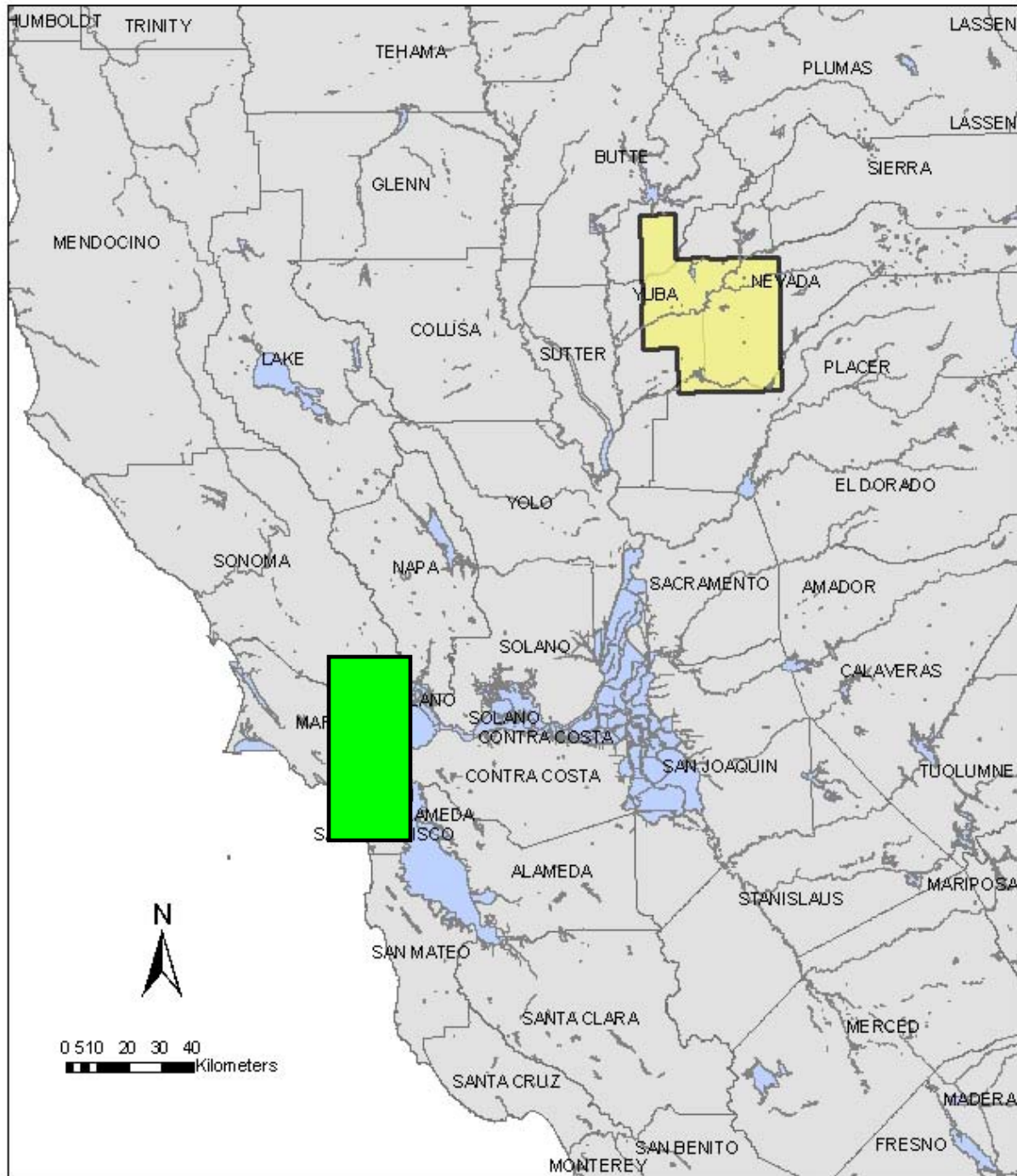


Figure 1: The green area indicates California black and Virginia rail population from San Francisco Bay, and yellow area indicates California black and Virginia rail population from Sierra Nevada foothills, California.

Thirteen additional Virginia rail feather samples were obtained from the museum specimens owned by the University of California, Berkeley, Museum of Vertebrate Zoology. These museum specimens were selected based on the proximity from the wetland sites in Sierra Nevada

foothills, as well as other regions where black and Virginia rails coexist. The museum specimens were initially collected between 1910 and 1953 (Appendix). Also, 21 feather samples from black rail were obtained from John A. Takekawa from the USGS Western Ecological Research Center, San Francisco Bay Estuary Field Station.

Both California black rail and Virginia rail molt their breast feather for both basic (winter) and alternate (breeding) plumage (Eddleman et al 1994, Taylor and Perlo 1998). Black rail go through a post breeding molt during July-August, and a pre-breeding molt during February-April. Virginia rail goes through a complete molt during July-August and pre-breeding molt in March. All feather samples were collected from rails captured during post breeding season from both foothills and San Francisco, with the exception of two samples obtained from the University of California, Berkeley, Museum of Vertebrate Zoology.

Feather preparation I first cleaned feathers with distilled water and then air dried them if there was dirt or foreign adherents. Then the feathers were cleaned in a 2:1 chloroform:methanol mixture to remove the natural oils on surface of the feathers (Hobson and Wassenaar 2008). The feathers were soaked in the mixture for at least 24 hours and then air dried in a fume hood for at least 24 hours.

I weighed the cleaned feathers in a microbalance and removed about 1.50 mg of feather material from each sample using small stainless steel surgical scissors. For samples where there were less than 1.50 mg of available feather materials, the sample contained at least 1.0 mg of feather material. For each sample, I cut the feather material into small pieces while the rachis of the feather was excluded since the rachis may contain isotope signature that might influence the overall signature of the feather (Hobson 2008). Then the sample was loaded into tin capsules (Costech, 3.5 x 5.0 mm) designed for elemental isotope analysis. The tin capsules were sealed shut by using tweezers to crimp the opening and folding down the capsule and compacted into a small spherical ball or cube. Then the compacted capsule was reweighed to record the final weight of the feather material contained in the capsule. A second tin capsule was used to ensure the feather samples were fully contained in the tin capsules to prevent contamination among samples. After the sample capsule was prepared, it was placed in the 96 position tray with the tray position and weight recorded. All utensils were cleaned between every sample using Kimwipes and methanol, and air dried briefly.

Isotopic Analysis The tin capsules that contains the sample were analyzed for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ with a ANCA-SL elemental analyzer coupled with a PDZ Europa Scientific 20-20 mass spectrometer (Europa Scientific, Vandalia, Ohio), at the University of California, Berkeley Center for Stable Isotope Biogeochemistry. Laboratory standards were used to express relative isotopic ratio for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. Atmospheric nitrogen is the standard used for $\delta^{15}\text{N}$, and Vienna-PeeDee Belemnite (V-PDB) is the standard used for $\delta^{13}\text{C}$. After the samples were analyzed, the isotopic ratios are expressed relative to the laboratory standards in parts per thousand (‰) using the δ notation. Stable isotope concentrations were expressed in δ notation according to the following formula:

$$\delta X = \left[\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right] \cdot 1000$$

X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. R_{standard} for ^{13}C and ^{15}N are the V-PDB standard and atmospheric nitrogen (AIR), respectively (Hobson and Clark 1992, Hobson and Wassenaar 2008).

All statistical analysis was carried out using JMP 8.0 (SAS Institute Inc., Cary, North Carolina). I used Wilcox-Mann Whitney test to determine if the mean of carbon and nitrogen isotope value differed between California black rail and Virginia rail, and among different black rail populations. A non-parametric test was used due to small and unequal sample size with non-normal distribution.

Results

Stable isotope analysis for carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) were ran from breast feather samples collected from a total of 34 California black rails and 11 Virginia rails from the Sierra Nevada foothills and San Francisco Bay (Table 1).

Table 1. Mean (\pm SD) stable-carbon and nitrogen isotope values for California black rail (BLRA) and Virginia rail (VIRA) from the Sierra Nevada foothills and San Francisco Bay.

	n	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)
Sierra Nevada foothills			
California black rail	13	8.6 ± 1.3	-22.3 ± 2.8
Virginia rail	7	9.3 ± 1.6	-24.2 ± 2.3

Species Wilcoxon-Mann Whitney		$p > 0.05$	$p > 0.05$
San Francisco Bay			
California black rail	21	16.4 ± 1.5	-22.2 ± 1.3
Virginia rail	4	12.6 ± 1.0	-24.0 ± 1.4
Species Wilcoxon-Mann Whitney		$p < 0.002^*$	$p < 0.02^*$
* significant, $p < 0.05$			

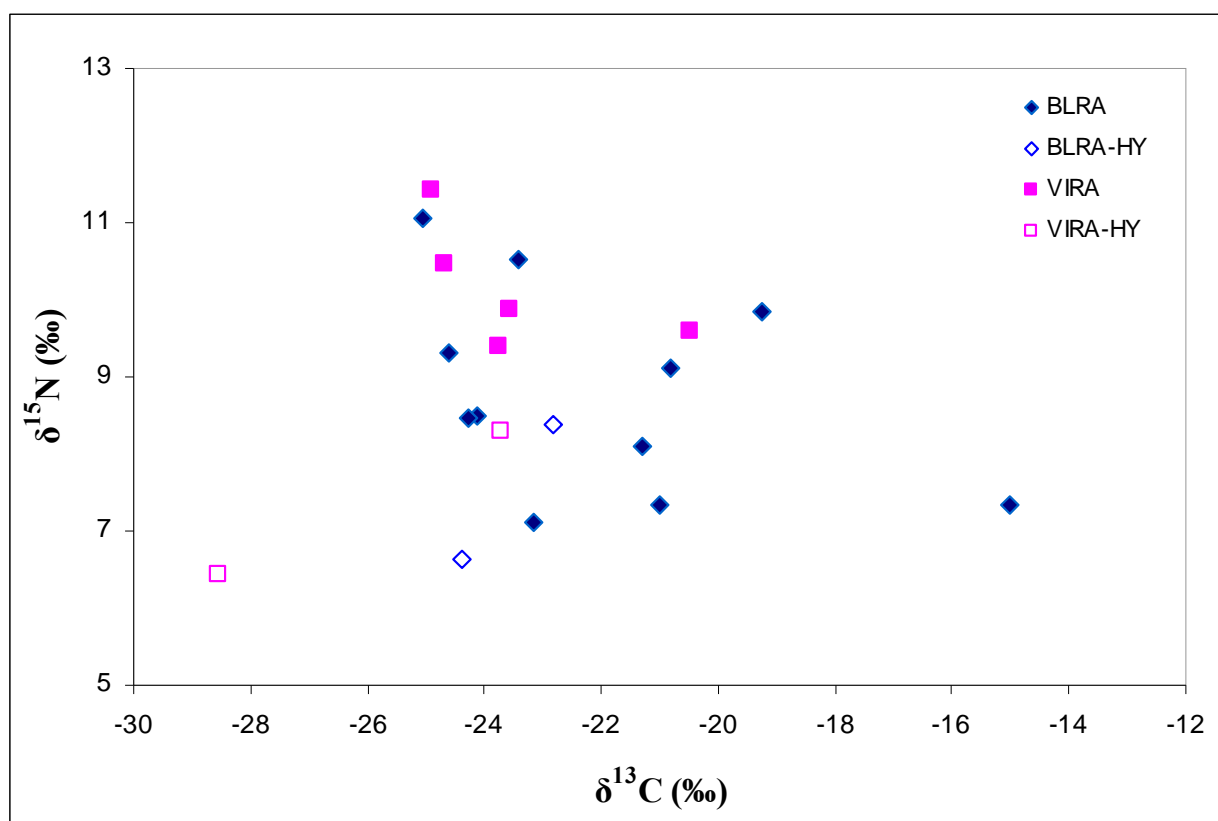


Figure 2. Stable isotope diagram of California black rail (BLRA) and Virginia rail (VIRA) feather signatures from the Sierra Nevada foothills. Juvenile rails (HY) are indicated with non filled symbols.

There is an overlap for the carbon and nitrogen isotope signatures of black and Virginia rail from Sierra foothills (Fig. 2). There is no significant difference found for both carbon ($P > 0.5$) and nitrogen ($P > 0.5$) isotope signatures between black and Virginia rails from Sierra foothills (Table 1). The mean $\delta^{13}\text{C}$ for California black rail and Virginia rail from the Sierra Nevada

foothills is -22.3‰ and -24.2‰ ($P > 0.5$), respectively (Table 1). The mean $\delta^{15}\text{N}$ for California black rail and Virginia rail is 8.6‰ and 9.3‰ ($P > 0.5$) respectively.

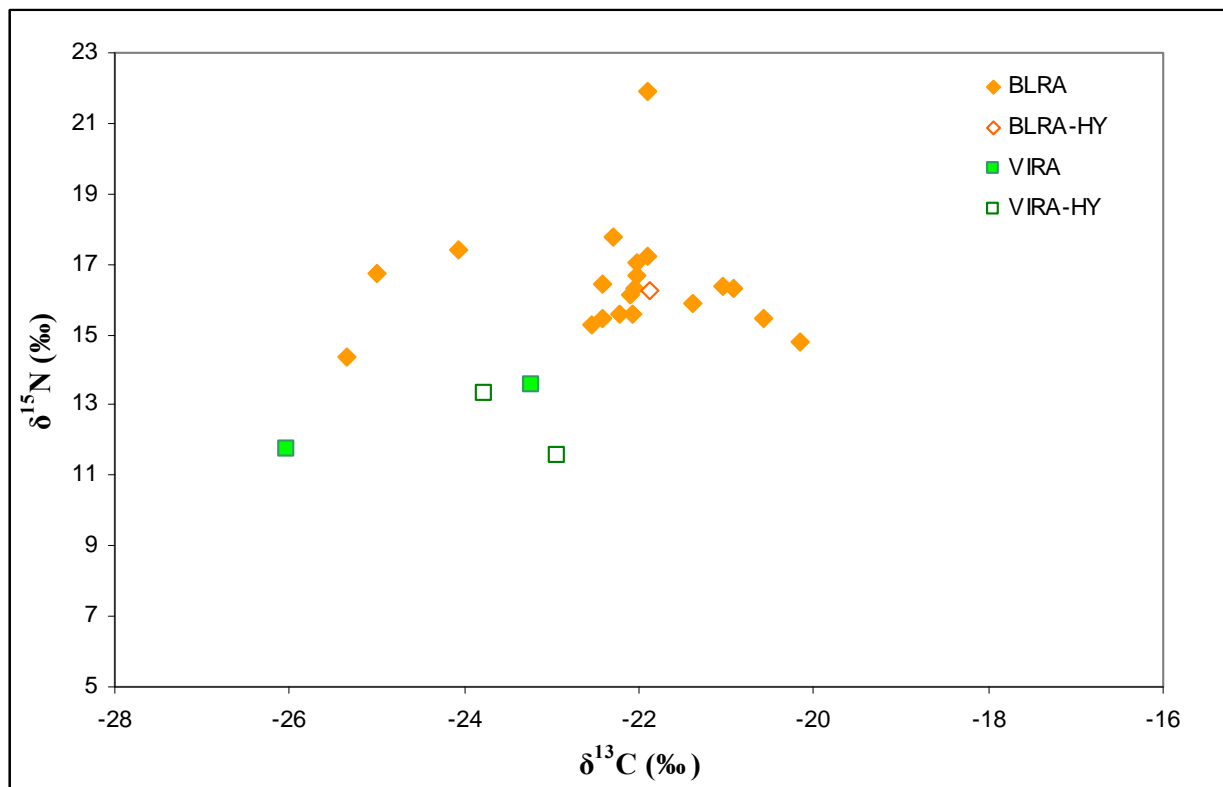


Figure 3. Stable isotope diagram of California black rail (BLRA) and Virginia rail (VIRA) feather signatures from the San Francisco population. Juvenile rails (HY) are indicated with non filled symbols.

There is some overlap for the carbon isotope signatures and no overlap for nitrogen isotope signature of black and Virginia rail from San Francisco Bay (Fig. 3). The difference is significant between black and Virginia rail for both carbon ($P < 0.02$) and nitrogen ($P < 0.002$) isotope signatures from San Francisco Bay (Table 1).

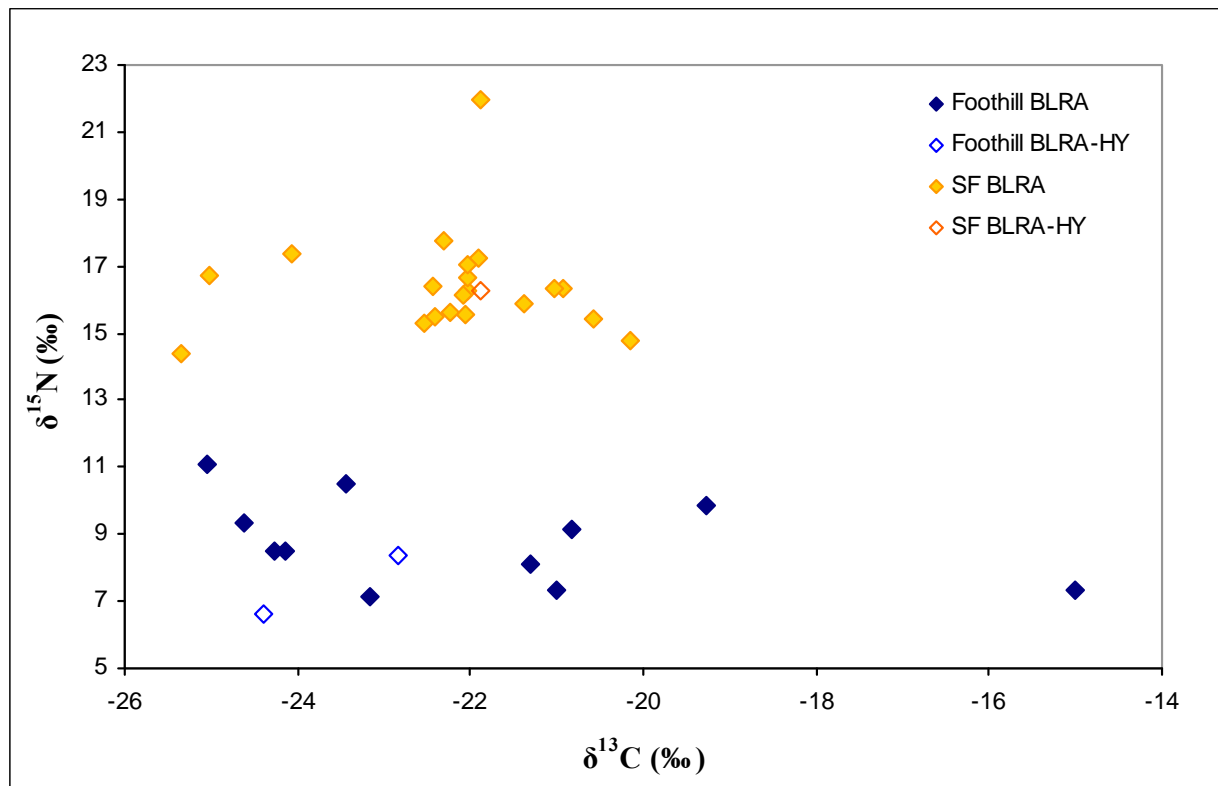


Figure 4. Stable isotope diagram of California black rail (BLRA) feather signatures from the Sierra foothills and San Francisco Bay population. Juvenile rails (HY) are indicated with non filled symbols.

There is some overlap for the carbon isotope signatures and no overlap for nitrogen isotope signature of black rails from Sierra foothills and San Francisco Bay (Fig. 4). The difference is significant for the nitrogen isotope signature ($P < 0.001$) and not significant for carbon ($P > 0.5$) isotope signatures between black rails from Sierra foothills and San Francisco Bay (Table 1).

Discussion

Does Virginia rail compete or partition food sources with California black rail in the Sierra Nevada foothills and San Francisco Bay? Based on the isotope analysis, there is no significant difference for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope signature between California black rail and Virginia rail from Sierra Nevada foothills (Table 1). This suggests that there is competition between the California black rail and Virginia rail in the Sierra foothills since the rails consumes food sources with similar carbon and nitrogen isotope signature. However, when comparing the isotope signature between black and Virginia rail from the San Francisco Bay, there is a significant different for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope signature. Based on the isotope analysis, this

suggests that black and Virginia rail from San Francisco Bay partition food sources. The discrepancy between the interaction for black and Virginia rail from Sierra foothill and San Francisco Bay may be due to regional differences and small sample size of Virginia rails from San Francisco Bay ($n = 4$).

Currently knowledge for the diet preferences of black and Virginia rail are mostly based on the stomach contents of the rails documented in previous studies. The diet information for the Virginia rails were better known than the black rails, since there was a larger sample size for Virginia rail compared with black rails. A study by Hoark (1970) recorded stomach content of 37 Virginia rail, and found that animal food predominates about 85-97% of the diet of Virginia rail during the summer (Hoark 1970). Virginia rails feed on mollusks, crayfish, amphipods, various insects and their larvae, spiders, small fish, frogs, and small snakes. Virginia rails also eat some aquatic plants and seeds of marsh plants. The study by Eddleman et al. (1994) found that black rail consumes mainly small aquatic and terrestrial invertebrates that are usually under 1 cm. The black rail eats predominantly animal food especially during breeding season, but black rail consumes more seeds during winter when insects are less available. Another study by Flores and Eddleman (1991) has collected diet information from seven California black rail based on the stomach contents. Black rails generally prefer terrestrial beetles, earwigs and ants based on the stomach contents.

Recent ecological studies have been focused on investigating how two species may occupy the same niche and exploit the same resources (Weller 1981). It has been found that species that compete for same resources may also specialize or develop mechanisms that reduce direct conflict with each other. It is likely Virginia rail compete for food items such as invertebrates with the black rail based on the stomach content and similarities in the nitrogen signature of the stable isotope analysis. However, it is also possible that Virginia rail may reduce this direct conflict with the black rail by consuming invertebrate and other food items that are found in deeper waters that are inaccessible by the black rails due to their morphological differences.

Do diet preferences of black rail population from Sierra Nevada foothills and San Francisco Bay differ? Based on the stable isotope analysis, there is a significant difference for $\delta^{15}\text{N}$ isotope signature but no significant difference for $\delta^{13}\text{C}$ isotope signature between black rail population from Sierra Nevada foothills and San Francisco Bay (Table 1). This suggests that the two black rail populations consume similar C3 plant diet but different animal diet. The black rail

population from San Francisco Bay have higher nitrogen isotope signature suggesting that the rails consume prey items from higher trophic level than the black rail population from Sierra foothills (Fig. 4). The difference in the nitrogen isotope signature is likely due to regional differences, that the coastal wetlands consist of more diverse and abundant prey items than inland freshwater wetlands. This may contribute to the higher nitrogen isotope values for the black rails from San Francisco Bay.

Small sample size from this study is potentially problematic especially for the isotope signature values obtained for the Virginia rail population. Also, one data point obtained from the juvenile Virginia rail and an adult black rail showed a large spread from the other data points obtained from the Sierra foothills population. Currently more sample is needed from population of black and Virginia rail from foothills to determine if the $\delta^{13}\text{C}$ isotope signature from the adult black rail and juvenile Virginia rail is an outlier.

Due to the time constraint and limitation of this study, isotope signature of potential rail food items was not collected for analysis. Future studies that analyze the isotopic signature of potential food sources will be able to better identify the exact diet of California and Virginia rails. Another limitation of my study is that it remains unclear how heavily the two rail species compete for food sources until additional feather samples are obtained. A larger sample size from Virginia rail will provide a better comparison of the isotope signatures with the California black rail.

By using stable isotope analysis to understand the diet information of the California black rail, it provides valuable information for conservation of the rail. Better diet information will allow management agencies to conserve California black rails through better managed wetland habitats that contain abundant food sources that are preferred by the California black rail. In addition, understanding the species interaction between the California black rail and Virginia rail improves our knowledge for the food web system for the wetlands where the two rail species coexist.

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References

- Aigner, P.A., J. Tecklin, and C.E. Koehler. 1995. Probable breeding population of the Black Rail in Yuba County, California. *Western Birds* 26: 157-160.
- Allen, J. A. 1990. The little black rail. *The Auk* 17: 1-8.
- Arizona Game and Fish Department. 2002. *Laterallus jamaicensis coturniculus*. Unpublished abstract compiled and edited by the Heritage Data Management System, Arizona Game and Fish Department, Phoenix, AZ. 5 pp.
- Beissinger, S. R., O.M. Richmond, and B. Risk. 2008. Temporal and spatial dimensions of colonization dynamics in two patch-tracking sympatric rail metapopulations. Unpublished project description for the black rail project. 15 pp.
- Conway, C. J. 1995. Virginia Rail. *In* The birds of North America, No. 173. A. Poole, and F. Gill, eds. The American Ornithologists' Union, Washington, D.C.
- Conway, C. J., and C. Sulzman. 2007. Status and habitat use of the California Black Rail in the southwestern USA. *Wetlands* 27. 987-998.
- Eddleman, W. R., R. E. Flores, and M. L. Legare. 1994. Black Rail (*Laterallus jamaicensis*). *In* The birds of North America, No. 123. A. Poole, and F. Gill, eds. The American Ornithologists' Union, Washington, D.C.
- Evens, J. G., G. W. Page, S. A. Laymon, R. W. Stallcup. 1991. Distribution, relative abundance and status of the California Black Rail in western north America. *The Condor* 93: 952-966.
- Flores, R. E. and W. R. Eddleman. 1991. Ecology of the California Black Rail in southwestern Arizona. Final Rept., U.S. Bur. Reclam., Yuma Proj. Off. and Arizona Dept. Game & Fish, Yuma, AZ. 15 pp.
- Flores, R. E., and W. R. Eddleman. 1995. California Black Rail use of habitat in Southwestern Arizona. *Journal of Wildlife Management* 59:357-363.
- Fry, B. 2006. *Stable Isotope Ecology*. Springer, New York. 308 pp.
- Hoefs, J. 2004. *Stable Isotope Geochemistry*. Springer, Berlin, New York. 244 pp.
- Hobson, K. A. and R. G. Clark. 1992. Assessing avian diets using stable isotopes II: factors affecting diet-tissue fractionation. *Condor* 94:189-197.
- Hobson, K.A. and L. I. Wassenaar. 2008. Tracking animal migration with stable isotopes, volume 2 in the terrestrial ecology series. Elsevier, San Diego. 144 pp.

- Horak, G. J. 1970. A comparative study of the foods of the Sora and Virginia Rail. *Wilson Bull.* 82:207-213.
- Kelly, J. F., and D. M. Finch. 1998. Tracking migrant songbirds with stable isotopes. *Trends in Ecology & Evolution* 13:48-49.
- Mizutani, H., M. Fukuda, and Y. Kabaya. 1992. C-13 enrichment and N-15 enrichment factors of feathers of 11 species of adult birds. *Ecology* 73:1391-1395.
- Newsome S. D, Martinez del Rio, C., Bearhop, S., and D. L. Phillips. 2007. A niche for isotopic ecology. *Frontiers in Ecology and the Environment* 5:429-436.
- Perkins, M. 2007. The use of stable isotopes to determine the ratio of resident to migrant King Rails in southern Louisiana and Texas. Master's Thesis. Louisiana State University, Baton Rouge, LA. 125 pp.
- Peterson and Fry. 1987. Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics* 18:293-320.
- Pospichal, L. B. 1952. A field study of Sora Rail (*Porzana Carolina*) and Virginia Rail (*Rallus limicola*) populations in central Minnesota. Master's Thesis. Univ. of Minnesota, St. Paul.
- Richmond, O.M. 2005. Final Report: Habitat relationships, distribution and metapopulation dynamics of the California Black Rail (*Laterallus jamaicensis coturniculus*) in the Sierra foothills. Prepared for the UC Davis Wildlife Health Center & California Department of Fish and Game Resource Assessment Program. 37 pp.
- Richmond, O. M., J. Tecklin, and S. R. Beissinger. 2008. Distribution of California Black Rails in the Sierra Nevada foothill. *J. Field Ornithol.* 79:381-390.
- Snider, P.R. 1969. Southwest region. *Audubon Field Notes* 23:681.
- Taylor, B. And B. V. Perlo. 1998. *Rails: a guide to the rails, crakes, gallinules and coots of the world*. Yale University Press, New Haven. 600 pp.
- Thompson, D. R. and R. W. Furness. 1995. Stable-isotope ratios of carbon and nitrogen in feathers indicate seasonal dietary shifts in northern fulmars. *The Auk* 112:493-498.
- Vanderklift, M. A. and S. Ponsard. 2003. Sources of variation in consumer-diet $\delta^{15}\text{N}$ enrichment: a meta-analysis. *Stable Isotope Ecology* 136:169-182.
- Wassenaar, L. I. and K. A. Hobson, K. A.. 2000b. Stable-carbon and hydrogen isotope ratios reveal breeding origins of red-winged blackbirds. *Ecological Applications* 10:911-916.
- Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes. 2002. Links between worlds: Unraveling migratory connectivity. *Trends in Ecology & Evolution* 17:76-83.

Weske, J. S. 1969. An ecological study of the Black Rail in Dorchester County, Maryland. Master's Thesis. Cornell Univ. Ithaca, NY.

Wilbur, S.R. 1974. The literature of the California Black Rails. 179. U.S. Department of the interior, Fish and Wildlife Service, Washington, D. C. 17 pp.