

1 Correspondence concerning this manuscript should be addressed to Alexandra Seelig,
2 Department of Wildlife Ecology & Conservation, University of Florida, 110 Newins-Ziegler
3 Hall, PO Box 110430, Gainesville, FL 32611-0430.
4 Contact phone: 269-405-3025
5 Contact email: aseelig@ufl.edu

6
7 Running heading: Stable isotopes reveal seasonal trophic niche variation

8
9 **Using stable isotope ratios to evaluate dietary breadth in *Oryzomys palustris sanibeli***

10

11 Alexandra L. Seelig*, Wesley W. Boone IV, and Robert A. McCleery

12

13 *Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL 32611,*
14 *USA (ALS, WWB, RAM)*

15

16 * *Correspondent: aseelig@ufl.edu*

17

18 The Sanibel Island rice rat (SIRR; *Oryzomys palustris sanibeli*) is a subspecies marsh rice rat
19 endemic to Sanibel Island, currently listed as a Species of Special Concern in the state of Florida.
20 Rice rats inhabit Sanibel's interior freshwater marshes, buttonwood shrublands [*Conocarpus*
21 *erectus*], and exterior mangrove swamps. The population of SIRR is estimated to be well under
22 100 individuals and little is known about their ecological niche. We examined stable isotope
23 ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of SIRR guard hair and samples of potential diet items to determine the

24 influence of seasonality (summer or winter) and habitat on trophic level and niche breadth. We
25 used Levene's test for homogeneity of variance to determine if SIRR dietary niche breadth
26 varied seasonally. Analysis showed that dietary niche breadth varied between summer and winter
27 samples for $\delta^{15}\text{N}$ ($p=0.018$) but not $\delta^{13}\text{C}$ ($p=0.068$), showing that SIRR diet was more diverse
28 during summer than winter periods. We found that SIRR isotopic ratios, using separate models
29 for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, overlapped with the animal prey base for $\delta^{15}\text{N}$ (f-value = 6.598, $p=0.014$) but
30 not $\delta^{13}\text{C}$ (f-value = 3.682, $p=0.062$), and showed no overlap with a plant prey base ($\delta^{13}\text{C}$ f-value
31 = 15.394, $p=0.0003$; $\delta^{15}\text{N}$ f-value = 9.241, $p=0.004$). Seasonality did not explain variation in
32 isotopic $\delta^{15}\text{N}$ (t-value = -0.328, $p = 0.745$) or $\delta^{13}\text{C}$ (t-value = 1.573, $p = 0.127$). These findings
33 show that SIRR significantly prefers animal prey items over plant diet items when available. As
34 such, we can conclude a food web ranking above that of primary consumers.

35

36 Key words: Florida, diet selection, *Oryzomys palustris sanibeli*, Sanibel Island, stable isotopes

37

38 **INTRODUCTION**

39 The Sanibel Island Rice Rat (SIRR, *Oryzomys palustris sanibeli*) is a subspecies of marsh rice
40 rat [*Oryzomys palustris*] endemic to Sanibel Island, Florida and listed by the State of Florida as a
41 Species of Special Concern (Hipes et al. 2000). The marsh rice rat (*Oryzomys palustris*) is a
42 semi-aquatic, medium-sized rat distributed throughout the Eastern United States, from
43 Pennsylvania to Florida, and west to Texas (Svihla 1931; Hamilton 1946; Esher et al. 1978;
44 Wolfe 1982). However, SIRR have evolved independently from other rice rat subspecies due to
45 geographic isolation, increasing the threat of extinction to this population (Indorf and Gaines
46 2013). Though it morphologically resembles other *Oryzomys* subspecies, *O. p. sanibeli* is
47 characterized by an amber brown pelage, an average body length of 263mm, tail length of
48 125mm, and 33mm hind foot (Hamilton 1955; Indorf and Gaines 2013).

49 While the life history of SIRR is not yet well-documented, much is known about the ecology
50 of other *O. palustris* populations. *O. palustris* has been suggested to be largely carnivorous
51 (Sharp 1967), while other sources have recorded a diet high in seeds and succulent plant parts
52 (Svihla 1931; Lowery 1974; Hamilton and Whitaker 1979). Negus et al. (1961) recorded a diet
53 ranging from 85% vegetation and seeds to 75% arthropods, with significant seasonal variation.
54 Insects, fiddler crabs, and snails are other common food items, as well as fish, clams, and the
55 carcasses of small birds or mammals (Lowery 1974; Hamilton and Whitaker 1979). Little is
56 known in comparison about plant diet items, but consumption of *Spartina alterniflora*, *Spartina*
57 *glabra*, *Salicornia europea*, *Tripsacum* sp., and *Elymus* sp. is presumed (Hamilton 1946).

58 These differences may be dependent on what foods are available. Presumably, flooded
59 periods offer increased carnivorous food sources because aquatic macroinvertebrates would be in
60 higher abundance, while dry periods may result in shifts towards plant food sources. This is of

61 particular interest on Sanibel Island which experiences distinct rainy, flooded (summer) and dry,
62 non-flooded (winter) seasons.

63 Due to these conflicting reports and the lack of specific knowledge on the SIRR, we
64 investigated the dietary breadth and diet item selection. We measured stable isotope ratios ($\delta^{13}\text{C}$
65 and $\delta^{15}\text{N}$), which are commonly used for evaluating trophic relationships and diet base, to
66 compare samples of SIRR guard hair samples in summer and winter with potential diet items.
67 Specifically, we tested four predictions: 1) SIRR would feed on a wider variety of diet items in
68 summer months compared to winter months due to greater availability of macroinvertebrates, 2)
69 SIRR feeds primarily on animal prey, in accordance with the findings of Sharp (1967) for
70 *Oryzomys palustris*, 3) SIRR found in freshwater grasslands would have isotopic signatures more
71 closely related to grass samples than those found in mangrove swamps, and 4) SIRR would
72 consume a greater amount of animal prey in mangrove wetlands than elsewhere due to the
73 limited diversity of plant species present.

74

75

MATERIALS AND METHODS

76 *Study area.*— Sanibel Island is a small (<4,900 ha) barrier island in southwest Florida (City
77 of Sanibel 2013). Conservation lands account for ~50% of the island, with remaining lands used
78 for residential development (City of Sanibel 2013). Remnant sand ridges ~1-2 m above mean sea
79 level trapped rainwater within the island's interior, creating freshwater wetlands with seasonally
80 variable water depths (Bogges 1974). A series of low ridges and swales occurred within the
81 island's interior creating a diversity of freshwater plant communities (City of Sanibel 2013).
82 Although historic accounts document nearly-continuous grasslands within the island's interior
83 (Hammond 1970), woody species have become dominant on many ridges. The freshwater

84 hydrology on Sanibel Island has been greatly altered by the construction of ponds and drainage
85 canals, elevated roads, and the filling of wetlands (Boggess 1974). Sanibel's mangrove forests,
86 while largely intact, have also experienced degradation due to mosquito control de-watering
87 projects. Historically, rice rats have been known to occur within these freshwater wetlands
88 (Humphrey et al. 1986), while recent research has uncovered their use of mangrove forests on
89 Sanibel Island (Boone, Unpublished data).

90 Sanibel Island lies within a tropical climate, with summers being significantly wetter than
91 winters, with fall to late spring only containing 15% of annual rainfall (Kushlan 1987; Duever et
92 al. 1994). Summers are characterized by frequent thunderstorms and occasional tropical cyclones
93 (Duever et al. 1994). Occasionally, winter frontal systems result in higher than average winter
94 rainfall (Duever et al. 1994). However, human alteration of the islands may significantly alter
95 hydroperiods of Sanibel's wetlands in comparison to other naturally-occurring wetlands (City of
96 Sanibel 2013). It is currently unknown how these hydroperiod variations impact SIRR
97 distribution (Abuzeineh et al. 2007; van der Merwe 2016).

98 For our research, we categorized SIRR habitats on the island into three distinct communities:
99 buttonwood shrublands, mangrove swamps, and inland grass marshes. The freshwater wetlands
100 make up much of the inland habitat for SIRR and consist of both ridges with short hydroperiods
101 and swales which remain dry for much of the year (City of Sanibel 2013). Swales are
102 characterized by water-dependent plant species and ridges contain more mesic species (Boone,
103 Unpublished data). Common freshwater wetland species in the region include cordgrasses
104 [*Spartina* sp.], sawgrasses [*Cladium* sp.], and leather ferns [*Acrostichum aureum*] (Boone,
105 Unpublished data). The buttonwood shrublands consist of wetland ridges that have transitioned
106 from grassy vegetation to woody species, especially buttonwood [*Conocarpus erectus*], in the

107 last eighty years (Hammond 1970). These buttonwood ridges are seasonally flooded, leading to a
108 transitional hydrologic profile (FNAI 2015). Coastal mangrove swamps are abundant on the
109 island, but SIRR has not been observed in these areas in the past (Florida Fish and Wildlife
110 Commission 2013). These swamps are characterized by red [*Rhizophora mangle*], black
111 [*Avicennia germinans*], and white mangroves [*Avicennia marina*] (Boone, Unpublished data).
112 We can refer to these communities as freshwater, transitional, and saltwater, respectively. We
113 classified collection sites into vegetative communities using vegetative data from the Florida
114 Natural Areas Inventory (Florida Natural Areas Inventory 2015) in ArcGIS.

115 *Data collection*— To understand the relationship between SIRR diet selection, seasonality,
116 and plant community we took hair samples from SIRR found in interior freshwater marshes,
117 buttonwood shrublands, and exterior mangrove swamps in summer and winter. We conducted
118 small mammal trapping on 54 grids located on conservation lands on Sanibel Island, Florida. We
119 placed 54 grids total, 18 grids in each of 3 communities; freshwater marshes, buttonwood
120 shrublands, and mangrove swamps. Each grid consisted of 25 Sherman box traps (8 cm × 9 cm ×
121 23 cm; H.B. Sherman Traps, Tallahassee, Florida, USA) in a 5x5 arrangement with 15m between
122 traps. We baited traps with birdseed and ran them for four consecutive nights at a time. We
123 collected approximately 1 cm² of dorsal guard hair to allow adequate material for stable isotope
124 analysis (Darimont & Reimchen 2002; van der Merwe and Hellgren 2016). To do this, we
125 scuffed each animal upon trapping and cut dorsal guard hair with scissors before releasing the
126 animal. We placed the hair in sterile plastic vials and froze until processing. We collected hair
127 samples during 2 trapping seasons (June-August 2017 and December 2017-February 2018). All
128 samples were collected from conservation lands in J.N. “Ding” Darling National Wildlife Refuge
129 on Sanibel Island, Florida as part of an ongoing study.

130 We chose hair for our stable isotope analysis to reflect a seasonal dietary turnover (Schwertl
131 et al. 2003; Sponheimer et al. 2003b; Cerling et al. 2006). Though SIRR hair molting frequencies
132 are currently unrecorded, we assumed a similar molting cycle to golden mice (*Ochrotomys*
133 *nuttali*) and deer mice (*Peromyscus* spp.). We only caught adult rats, allowing us to operate on
134 the assumption of biannual adult molts in the spring and fall (Linzey and Linzey 1967; Miller et
135 al. 2008). By these assumptions and because we sampled in summer and winter, hair samples can
136 be used to estimate diet over the prior 2-4 months, since the most recent spring/winter molt.

137 We collected potential food items from each area including vegetation, epifauna, fish, and
138 macroinvertebrates. Due to increased availability in both macroinvertebrate and plant diet items,
139 we chose to collect diet items in the summer season. We clipped vegetation and used mesh dip
140 nets to sample for macroinvertebrates, fish, and insects in each of 3 sampling communities
141 because these items are known components of SIRR diets (van der Merwe and Hellgren 2016).
142 Invertebrates included insects (mostly dragonflies, damselflies, aquatic beetles and all within the
143 orders Hemiptera, Coleoptera and Odonata), gastropods (from families Littorinidae, Ellobiidae,
144 Thiaridae and Mytilidae) and crustaceans (mangrove crabs, crayfish, and fiddler crabs from
145 families Sesarmidae, Cambaridae, and Ocypodidae, respectively). Vertebrates included fish
146 (*Gambusia* and *Poecilia*) and anoles (*Anolis sagrei*). Vegetation samples included mangrove
147 shoots [*Avicennia germinans*; *A. marina*; *Rhizophora mangle*], vines or propagules, buttonwood
148 [*Conocarpus erectus*], sedges [family Cyperaceae], cordgrasses [*Spartina* sp.], purslane [family
149 Portulacaceae], sawgrass [*Cladium* sp.], and flowering plants including *Tillandsia recurvata*,
150 *Eustoma exaltatum*, *Bacopa monnieri* and *Parthenocissus quinquefolia*.

151 We developed sampling processing protocol in accordance with van der Merwe and Hellgren
152 (2016). We froze samples within 6 hours of collection except for hair samples which we stored at

153 ambient temperature. We stored macroinvertebrate samples in ethanol for identification before
154 being processed. We soaked hair in an acetone bath for 2 hours and we rinsed all samples for 10
155 minutes in deionized water before drying them for 72 hours at 60°C. Following oven drying, we
156 also dried and ground some samples in a cryogenic freezer mill. We homogenized and ground
157 the remainder of the samples with a mortar and pestle. We stored subsamples (~2.0mg for
158 vegetation; ~0.35–0.45 mg for hair and invertebrates) in glass vials while waiting for isotopic
159 analysis. This work was authorized by the University of Florida’s Institutional Animal Care and
160 Use Committee (IACUC; Protocol 201709811). We then analyzed stable isotope ratios of hair
161 and food samples ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) to test seasonal niche breadth variation and to investigate
162 typical trophic level of SIRR in each community.

163 *Stable isotope analysis.*— To understand relationships between rice rats, diet items, and
164 season, we applied $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values to our samples. Values of $\delta^{15}\text{N}$ from animal tissue
165 samples reveal the nitrogen isotopic composition of the animal’s diet items with 3-4%
166 enrichment, with values increasing as trophic level increases (DeNiro and Epstein 1981;
167 Minagawa and Wada 1984; Peterson and Fry 1987). The $\delta^{15}\text{N}$ values also serve to elucidate
168 complex food web interactions that otherwise are difficult to quantify (Kling et al. 1992).
169 Conversely, $\delta^{13}\text{C}$ levels remain stable between trophic positions but vary among primary
170 producers, and by extension, organisms feeding on primary producers (Rounick and Winterbourn
171 1986; Peterson and Fry 1987; France and Peters 1997). In terrestrial systems, $\delta^{13}\text{C}$ can also be
172 used to discriminate between vegetation characterized by different photosynthetic pathways (C_3
173 vs. C_4 vs. CAM) and therefore, is useful for further characterizing the nature of plants in a diet
174 (Rounick and Winterbourn 1986; Peterson and Fry 1987; O’Leary et al. 1992). Because C_3
175 plants discriminate against ^{13}C more than C_4 plants, a higher ratio of ^{13}C to ^{12}C (denoted as $\delta^{13}\text{C}$)

176 in hair samples would indicate a diet higher in C4 plants like grasses and sedges (Sponheimer et
177 al. 2003a). However, we cannot use these values alone to determine trophic level without
178 appropriate isotopic baselines for comparison purposes (Post 2002).

179 Samples were analyzed at the University of Florida Light Stable Isotope Mass Spectrometry
180 Lab using a Thermo Electron DeltaV Advantage isotope ratio mass spectrometer coupled with a
181 ConFlo II interface linked to a Carlo Erba NA 1500 CNHS Elemental Analyzer. Samples were
182 loaded into tin capsules and placed in a 50-position automated Zero Blank sample carousel on a
183 Carlo Erba NA1500 CNS elemental analyzer. After combustion in a quartz column at 1020°C in
184 an oxygen-rich atmosphere, the sample gas was transported in a He carrier stream and passed
185 through a hot reduction column (650°C) consisting of elemental copper to remove oxygen. The
186 effluent stream then passed through a chemical (magnesium perchlorate) trap to remove water
187 followed by a 0.7 meter GC column at 120°C to separate N₂ from CO₂. The sample gas next
188 passed into a ConFlo II preparation system and into the inlet of a Thermo Electron Delta V
189 Advantage isotope ratio mass spectrometer running in continuous flow mode where the sample
190 gas was measured relative to laboratory reference N₂ and CO₂ gases. All carbon isotopic
191 results are expressed in standard delta notation relative to VPDB. All nitrogen isotopic results
192 are expressed in standard delta notation relative to AIR (Curtis, personal communication).

193 *Data analysis.*— We investigated a metric of trophic niche breadth by quantifying the
194 variance of stable isotopic values among-individuals (Bearhop et al. 2004). We compared stable
195 isotopic niche breadth of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ between SIRR summer and winter samples, and between
196 samples collected in each of the 3 vegetative communities, using Levene's test of homogeneity
197 of variance (Flaherty and Ben-David 2010). We used Levene's test of homogeneity to infer
198 whether $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotopic ratios overlapped sampled plant and animal prey items. We

199 assumed that a smaller breadth of variance was the result of specialization on a limited number
200 of food sources, and larger variance resulted from a more generalist diet. For all analyses, we
201 used hair-to-diet discrimination factors of 1‰ C and 3‰ N (Steenweg et al. 2011; Weiser and
202 Powell 2011; Osterback et al. 2015). We also investigated whether vegetative community
203 explained variation in isotopic $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ between samples (separate models for $\delta^{15}\text{N}$ and
204 $\delta^{13}\text{C}$) using a Tukey-Kramer Pairwise Multiple Comparison Test to account for unequal sample
205 sizes between groups (Sokal and Rohlf 1995). We also used generalized linear models,
206 separately for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (van der Merwe and Hellgren 2016), in program R (R version 3.4.2,
207 www.r-project.org, accessed 4 March 2017) to determine if seasonality explained variation in
208 isotopic $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ sample values.

209

210 **RESULTS**

211 We collected 15 SIRR hair samples in summer and 15 in winter. Of these, we collected
212 23, 5, and 2 hair samples from freshwater marshes, buttonwood shrublands, and mangrove
213 swamps, respectively. We collected 28 plant and 19 animal specimens for isotopic analysis. We
214 averaged isotopic values when multiple samples of a single species were available so that only 1
215 value was used in the statistical analyses. This yielded 25 plant and 15 animal specimens
216 included in statistical analyses.

217 Rice rat fur isotopic ratios were found to overlap with that of an animal prey base for
218 $\delta^{13}\text{C}$ (f-value = 3.682, p=0.062), but differed significantly for $\delta^{15}\text{N}$ (f-value = 6.598, p=0.014).
219 Fur isotopic ratios differed significantly from a plant food base ($\delta^{13}\text{C}$ f-value = 15.394,
220 p=0.0003; $\delta^{15}\text{N}$ f-value = 9.241, p=0.004; Fig. 1). Hair sample $\delta^{15}\text{N}$ varied significantly
221 between summer (mean = 5.37) and winter (mean = 5.51, p=0.018), while $\delta^{13}\text{C}$ did not (summer

222 mean = -23.06, winter mean = -23.86, $p=0.068$; Fig. 2). Vegetative community modeled using a
223 Tukey-Kramer Pairwise Multiple Comparison Test was significantly correlated with $\delta^{13}\text{C}$
224 isotopic ratios for pairwise comparisons because the 95% confidence interval (CI) was positive
225 and did not pass through zero for freshwater marsh-buttonwood shrubland (mean = 1.604, CI =
226 0.3-2.909) and buttonwood shrubland-mangrove swamp (mean = 4.375, CI = 2.164-6.587), but
227 not for mangrove swamp-freshwater marsh whose CI contained zero (mean = -2.771, CI = -
228 4.720—0.822; Fig. 3). There was no significant effect for $\delta^{15}\text{N}$ isotopic ratio pairwise
229 comparisons between any vegetative communities because all comparisons crossed zero
230 (freshwater marsh-buttonwood shrubland mean = -0.566, 95 CI = -1.963-0.831; buttonwood
231 shrubland-mangrove swamp mean = -1.526, CI = -3.895-0.842; mangrove swamp-freshwater
232 marsh mean = 0.96, CI = -1.127-3.047). Seasonality did not explain variation in isotopic $\delta^{15}\text{N}$ (t-
233 value = -0.328, $p = 0.745$) or $\delta^{13}\text{C}$ (t-value = 1.573, $p = 0.127$).

234

235

DISCUSSION

236

237

238

239

240

241

242

243

As predicted, SIRR isotopic values indicated a diet higher in animal prey than vegetation, regardless of season or community. These findings were in agreement with those in Sharp (1967) that rice rats are primarily carnivorous when animal prey items are available. However, animal prey items found in mangrove areas (crabs, snails, etc) had high $\delta^{13}\text{C}$ values (>-18), in line with those of grassland vegetation, that were not detected in the hair of rodents from mangrove areas indicating a potential avoidance of animal food sources in mangrove areas. Therefore, it appears that most reliance on animal prey occurs in Sanibel's freshwater wetlands, not in mangrove wetlands as we had predicted. This emphasis on freshwater animal prey is worrisome for a

244 barrier island frequently impacted by hurricanes and that is vulnerable to rising sea levels (Titus
245 1990).

246 We also found that SIRR diet breadth variance does indeed vary seasonally as we
247 predicted. Variation of winter isotopic ratios (both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in hair samples was less than
248 that of summer samples. This wide summer scatter confirms that SIRR diet is much broader and
249 more diverse in summer months than in winter months. This may indicate seasonal variation in
250 their reliance on macroinvertebrates (high $\delta^{15}\text{N}$ values) which are presumably more abundant
251 during wet summer months, and a greater abundance and diversity of plant food sources in
252 summer (low $\delta^{15}\text{N}$ values) (Neckels et al. 1990). If macroinvertebrate populations decrease in
253 drier months, SIRR would be forced to consume more plants, especially grasses and sedges,
254 leading to a more consistent diet profile across all sites (Neckels et al. 1990).

255 Finally, we found that hair isotopic $\delta^{13}\text{C}$ composition varied significantly depending on the
256 community in which they were caught (Fig. 3.). Because C4 plants like grasses and sedges favor
257 the heavier ^{13}C compared to C3 plants, C4 plants will exhibit a higher $\delta^{13}\text{C}$ ratio in the hair
258 samples (Sponheimer et al. 2003a). The lower values of $\delta^{13}\text{C}$ came from hair samples collected
259 in the mangrove swamps, so we can conclude that that population shows the least signature of a
260 grass-based diet. SIRR caught in grassy freshwater marshes show a comparatively stronger grass
261 diet signature as the $\delta^{13}\text{C}$ are higher than those in mangrove swamps. However, SIRR trapped in
262 the buttonwood shrubland (transitional) areas exhibited higher $\delta^{13}\text{C}$ values and therefore had a
263 larger signature of a grass diet than those caught in the grasslands. This may be because
264 grasslands are flooded more frequently, and therefore likely support a greater abundance and
265 diversity of macroinvertebrate and fish prey. Therefore, SIRR occupying grasslands eat more
266 animals and less grass than those in the buttonwood shrubland. Furthermore, this may indicate

267 that SIRR selectively choose C4 plants (grasses over other vegetation types) in the shrublands
268 that may be more prevalent.

269 Additionally, the lack of overlap between SIRR hair isotopic ratios in different vegetative
270 communities implies that movement between these areas may be limited. This finding is
271 noteworthy because it indicates that multiple populations of SIRR may occur separately on
272 Sanibel Island and maintain foraging area fidelity, increasing the likelihood of local extirpation.
273 It is not known if movements are restricted as a result of anthropogenic alteration of the island
274 (i.e. isolation by roads, development, canals, etc).

275 Our findings suggest that SIRR are capable of exploiting seasonally available food
276 sources, with dietary breadth maximized during summer months when much of the island is
277 inundated with fresh water. Animal prey is likely an important dietary component during all
278 seasons, in accordance with Sharp (1967). Further research regarding the effects of water level
279 modification on aquatic invertebrate diversity and abundance are needed to ensure adequate prey
280 levels are maintained. Finally, the apparent lack of movement of rice rats between various habitat
281 types, at least over time spans of 3-4 months, requires further investigation to determine if
282 dispersal barriers have been induced by anthropogenic change.

283

284 **ACKNOWLEDGMENTS**

285 We thank University of Florida's University Scholars Program and Undergraduate Honors
286 Program, U.S. Fish and Wildlife Service, and Florida Fish and Wildlife Conservation
287 Commission for funding this research. We thank J.N. "Ding" Darling National Wildlife Refuge,
288 Sanibel-Captiva Conservation Foundation, the City of Sanibel, and The Sanctuary Golf Club for
289 their collaborative efforts and property access. We thank the Ding Darling Wildlife Society for

290 providing housing throughout our research. Individually, we would like to thank Audrey
291 Albrecht, Jennifer Bernatis, Joelle Carbonell, Nate Caswell, Mark Clark, Jeremy Conrad, Jason
292 Curtis, Sarah Lathrop, Chris Lechowicz, Holly Milbrandt, Birgie Miller, Tre’Nard Morgan, Kyle
293 Sweet, Paul Tritaik, and Toni Westland,

294

295 **LITERATURE CITED**

296

297 Abuzeineh, A. A., R. D. Owen, N. E. McIntyre, C. W. Dick, R. E. Strauss, and T. Holsomback.
298 2007. Response of marsh rice rat (*Oryzomys palustris*) to inundation of habitat.
299 *Southwestern Naturalist* 52:75-78.

300

301 Bearhop, S., Adams, C. E., Waldron, S., Fuller, R. A. and Macleod, H. 2004. Determining
302 trophic niche width: a novel approach using stable isotope analysis. *Journal of Animal*
303 *Ecology* 73: 1007–1012.

304

305 Brown, L. N. 1997. *Mammals of Florida*. Windward Publishing Inc., Miami.

306

307 Boggess, D. H. 1974. The shallow fresh-water system of Sanibel Island, Lee County, Florida,
308 with emphasis on the sources and effects of saline water. Florida Bureau of Geology
309 Report of Investigation 69. Tallahassee, Florida.

310

311 Cerling, T. E., G. Wittemyer, H. B. Rasmussen, F. Vollrath, C. E. Cerling, T. J. Robinson, and I.
312 Douglas-Hamilton. 2006. Stable isotopes in elephant hair document migration patterns
313 and diet changes. *Proceedings of the National Academy of Sciences, USA* 103:371–373.
314

315 City of Sanibel. 2013. Sanibel plan: the comprehensive land use plan of the City of Sanibel,
316 Florida. Sanibel, Florida.
317

318 Darimont, C. T., and T. E. Reimchen. 2002. Intra-hair stable isotope analysis implies seasonal
319 shift to salmon in gray wolf diet. *Canadian Journal of Zoology* 80:1638–1642.
320

321 DeNiro, M. J., and S. Epstein. 1978. Influence of diet on the distribution of carbon isotopes in
322 animals. *Geochimica et Cosmochimica Acta* 42:495–506.
323

324 DeNiro, M. J., and S. Epstein. 1981. Influence of diet on the distribution of nitrogen isotopes in
325 animals. *Geochimica et Cosmochimica Acta* 45:341–351.
326

327 Duever, M. J., Meeder, J. F., Meeder, L. C., & McCollom, J. M. 1994. The climate of south
328 Florida and its role in shaping the Everglades ecosystem. *Everglades: The ecosystem and*
329 *its restoration*, 225-248.
330

331 Ellstrand, N.C., and D.R. Elam. 1993. Population genetic consequences of small population size:
332 Implications for plant conservation. *Annual Review of Ecology and Systematics* 24:217-
333 242.

334

335 Esher, R.J., J. L. Wolfe, and J. N. Layne. 1978. Swimming Behavior of Rice Rats (*Oryzomys*
336 *palustris*) and Cotton Rats (*Sigmodon hispidus*), *Journal of Mammalogy* 59(3):551-8.

337

338 Flaherty, E. A., and M. Ben-David. 2010. Overlap and partitioning of the ecological and isotopic
339 niches. *Oikos* 119:1409-1416.

340

341 Florida Fish and Wildlife Conservation Commission. 2013. A species action plan for the Sanibel
342 Island rice rat. Tallahassee, Florida.

343

344 Florida Natural Areas Inventory. 2015. Cooperative land cover map. Tallahassee, Florida.

345

346 France, R. L., and R. H. Peters. 1997. Ecosystem differences in the trophic enrichment of ¹³C in
347 aquatic food webs. *Canadian Journal of Fisheries and Aquatic Sciences* 54:1255–1258.

348

349 Goldman, E. A. 1918. The rice rats of North America. *North American Fauna* 43:1–100.

350

351 Hamilton, W. 1946. Habits of the Swamp Rice Rat, *Oryzomys Palustris Palustris* (Harlan). The
352 *American Midland Naturalist* 36(3):730-736.

353

354 Hamilton, W. J. 1955. Two new rice rats (genus *Oryzomys*) from Florida. *Proceedings of the*
355 *Biological Society Washington* 68:83– 86.

356

357 Hamilton, Jr., W. J. and J. O. Whitaker, Jr. 1979. Mammals of the eastern United States. Second
358 Ed. Cornell University Press.
359

360 Hammond, E. A. 1970. Sanibel Island and its vicinity, 1833, a Document, The Florida Historical
361 Quarterly 48:392-411.
362

363 Hipes, D., Jackson, D. R., NeSmith, K., Printiss, D., & Brandt, A. 2000. Field guide to the rare
364 animals of Florida. Florida Natural Areas Inventory, Tallahassee, Florida.
365

366 Humphrey, S. R., R. W. Repenning, and H. W. Setzer. 1986. Status survey of five Florida
367 mammals. University of Florida Cooperative Fish and Wildlife Research Unit, Technical
368 Report No. 22, Gainesville, Florida.
369

370 Indorf, J.L. & Gaines, M.S. 2013. Genetic divergence of insular marsh rice rats in subtropical
371 Florida. Journal of Mammalogy 94(4):897-910.
372

373 Kling, G. W., B. Fry, and W. J. O'Brien. 1992. Stable isotopes and planktonic trophic structure
374 in arctic lakes. Ecology 73:561-566.
375

376 Kushlan, J. A. 1987. External threats and internal management: the hydrologic regulation of the
377 Everglades, Florida, USA. Environmental Management 11:109-119.
378

379 Linzey, D. W., and A. V. Linzey. 1967. Maturational and seasonal molts in the golden mouse,
380 *Ochrotomys nuttalli*. Journal of Mammalogy 48:236–241.
381

382 Lowery, G. H. 1974. Mammals of Louisiana and its adjacent waters. Louisiana State Univ. Press,
383 Baton Rouge.
384

385 Miller, J. F., J. S. Millar, and F. J. Longstaffe. 2008. Carbon- and nitrogen-isotope tissue–diet
386 discrimination and turnover rates in deer mice, *Peromyscus maniculatus*. Canadian
387 Journal of Zoology 86: 685–691
388

389 Minagawa, M., and E. Wada . 1984. Stepwise enrichment of ^{15}N along food chains: further
390 evidence and the relation between ^{15}N and animal age. Geochimica et Cosmochimica
391 Acta 48:1135–1140.
392

393 Myers, D. 2010. Oxygen and hydrogen stable isotope ratios in Mississippi River floodplain
394 invertebrates: implications for dispersal and food web analysis. Thesis. Southern Illinois
395 University, Carbondale, Illinois, USA.
396

397 Neckles, H. A., Murkin, H. R., & Cooper, J. A. 1990. Influences of seasonal flooding on
398 macroinvertebrate abundance in wetland habitats. Freshwater Biology, 23(2):311-322.
399

400 Negus, N. C., Gould, E., & Chipman, R. K. 1961. Ecology of the rice rat, *Oryzomys palustris*
401 (Harlan), on Breton Island, Gulf of Mexico, with a critique of the social stress
402 theory. *Tulane Studies in Zoology* 8(4):95-123.
403

404 Nifong, J.C., Layman, C.A., & Silliman, B.R. 2015. Size, sex and individual-level behaviour
405 drive intrapopulation variation in cross-ecosystem foraging of a top-predator. *Journal of*
406 *Animal Ecology* 84:35-48.
407

408 O'Leary, M. H., S. Madhavan, and P. Paneth. 1992. Physical and chemical basis of carbon
409 isotope fractionation in plants. *Plant, Cell and Environment* 15:1099–1104.
410

411 Osterback, A. K., D. M. Frechette, S. A. Hayes, S. A. Schaffer, and J. W. Moore. 2015. Long-
412 term shifts in anthropogenic subsidies to gulls and implications for imperiled fish.
413 *Biological Conservation* 191:606–613.
414

415 Peterson, B. J., and B. Fry. 1987. Stable isotopes in ecosystem studies. *Annual Review of*
416 *Ecology and Systematics* 18:293–320.
417

418 Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and
419 assumptions. *Ecology* 83:703–718.
420

421 Rounick, J. S., and M. J. Winterbourn. 1986. Stable carbon isotopes and carbon flow in
422 ecosystems. *BioScience* 36:171–177.

423

424 Schwertl, M., K. Auerswald, and H. Schnyder. 2003. Reconstruction of the isotopic history of
425 animal diets by hair segmental analysis. *Rapid Communications in Mass Spectrometry*
426 17:1312–1318.

427

428 Sharp Jr., H. F. 1967. Food ecology of the rice rat, *Oryzomys palustris* (Harlan), in a Georgia salt
429 marsh. *Journal of Mammalogy* 48(4):557-563.

430

431 Sokal, R., and F. Rohlf. 1995. *Biometry*. 3rd edition. Freedman and Company, New York.

432

433 Spitzer, N. C., AND J. D. Lazell, Jr. 1978. A new rice rat (genus *Oryzomys*) from Florida's
434 Lower Keys. *Journal of Mammalogy* 59:787–792.

435

436 Sponheimer, M., Lee-Thorp, J.A., DeRuiter, D.J., Smith, J.M., Van Der Merwe, N.J., Reed, K.,
437 Grant, C.C., Ayliffe, L.K., Robinson, T.F., Heidelberger, C. and Marcus, W. 2003. Diets
438 of southern African Bovidae: stable isotope evidence. *Journal of Mammalogy* 84(2):471-
439 479.

440

441 Sponheimer, M., T. Robinson, L. Ayliffe, B. Roeder, J. Hammer, B. Passey, A. West, T. Cerling,
442 D. Dearing, and J. Ehleringer. 2003. Nitrogen isotopes in mammalian herbivores: hair
443 $\delta^{15}\text{N}$ values from a controlled feeding study. *International Journal of Osteoarchaeology*
444 13:80–87.

445

446 Steenweg, R. J., R. A. Ronconi, and M. L. Leonard. 2011. Seasonal and age-dependent dietary
447 partitioning between great black-backed and herring gulls. *The Condor* 113:795–805.
448

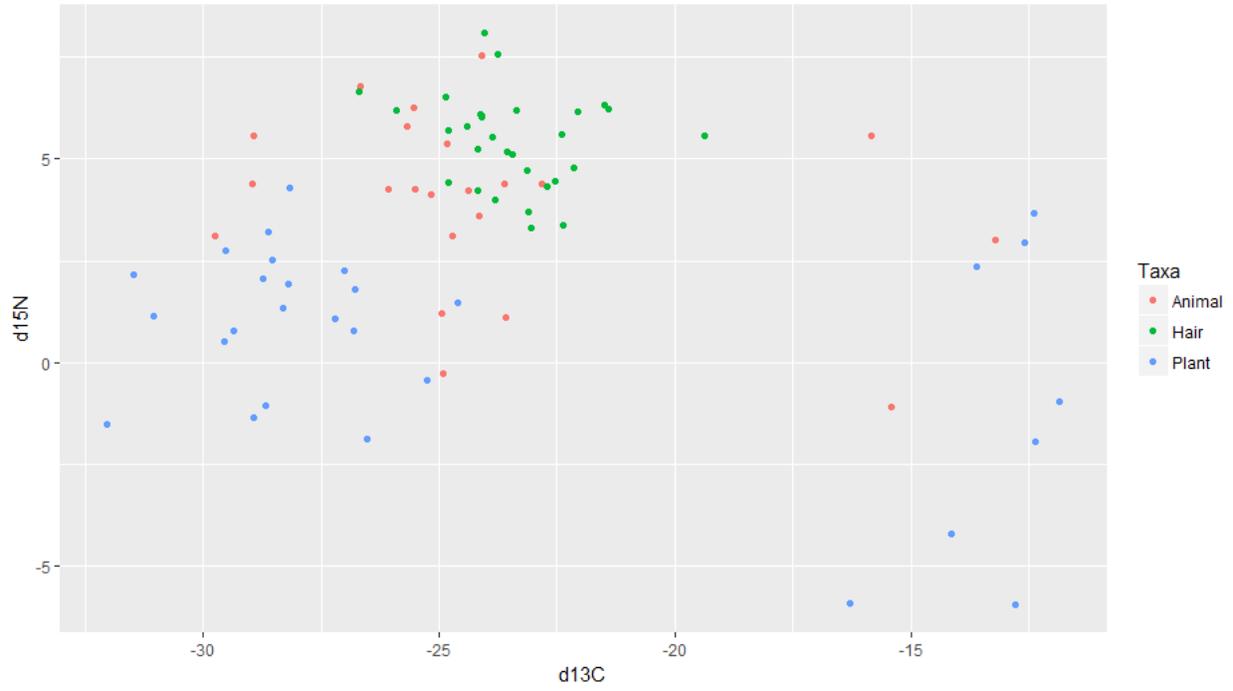
449 Svihla, A. 1931. Life History of the Texas Rice Rat (*Oryzomys palustris texensis*). *Journal of*
450 *Mammalogy* 12(3):238-242.
451

452 Titus, J. G. 1990. Greenhouse effect, sea level rise, and barrier islands: Case study of Long
453 Beach Island, New Jersey.
454

455 Van der Merwe, J., and E. C. Hellgren. 2016. Spatial variation in trophic ecology of small
456 mammals in wetlands: support for hydrological drivers. *Ecosphere* 7:e01567.
457

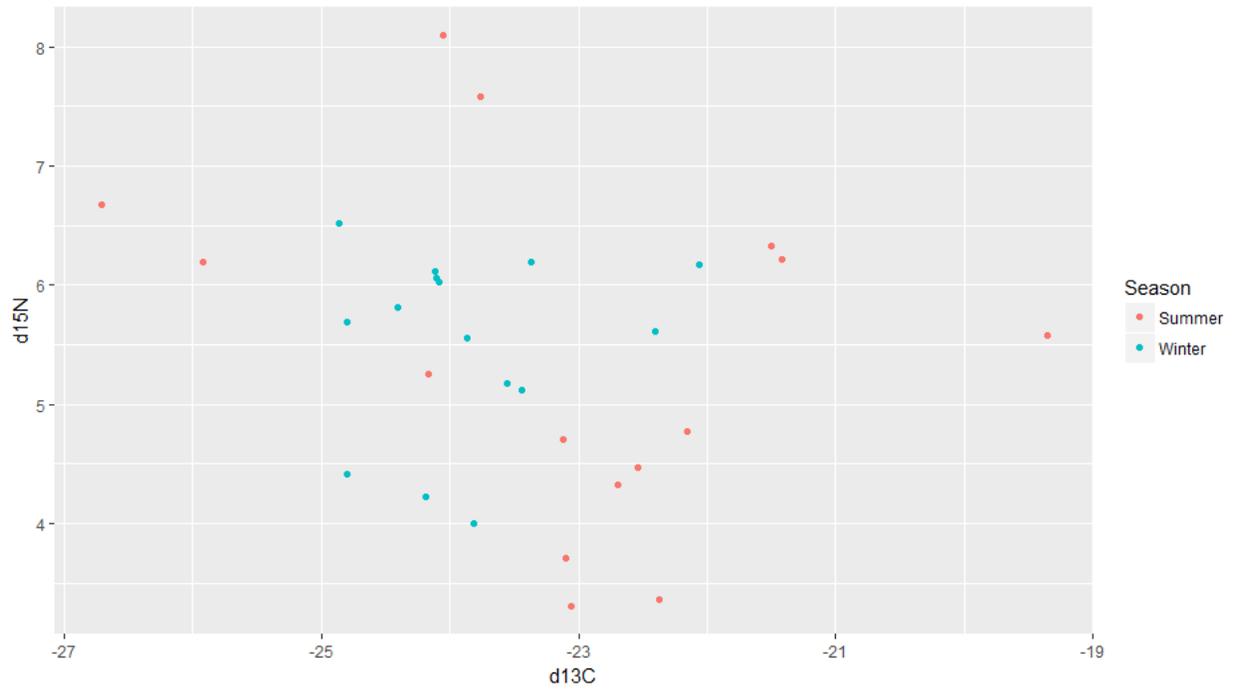
458 Weiser, E. L., and A. N. Powell. 2011. Evaluating gull diets: a comparison of conventional
459 methods and stable isotope analysis. *Journal of Field Ornithology* 82:297–310
460

461 Wolfe, J. L. 1982. *Oryzomys palustris*. *Mammalian Species* 176:1–5.
462



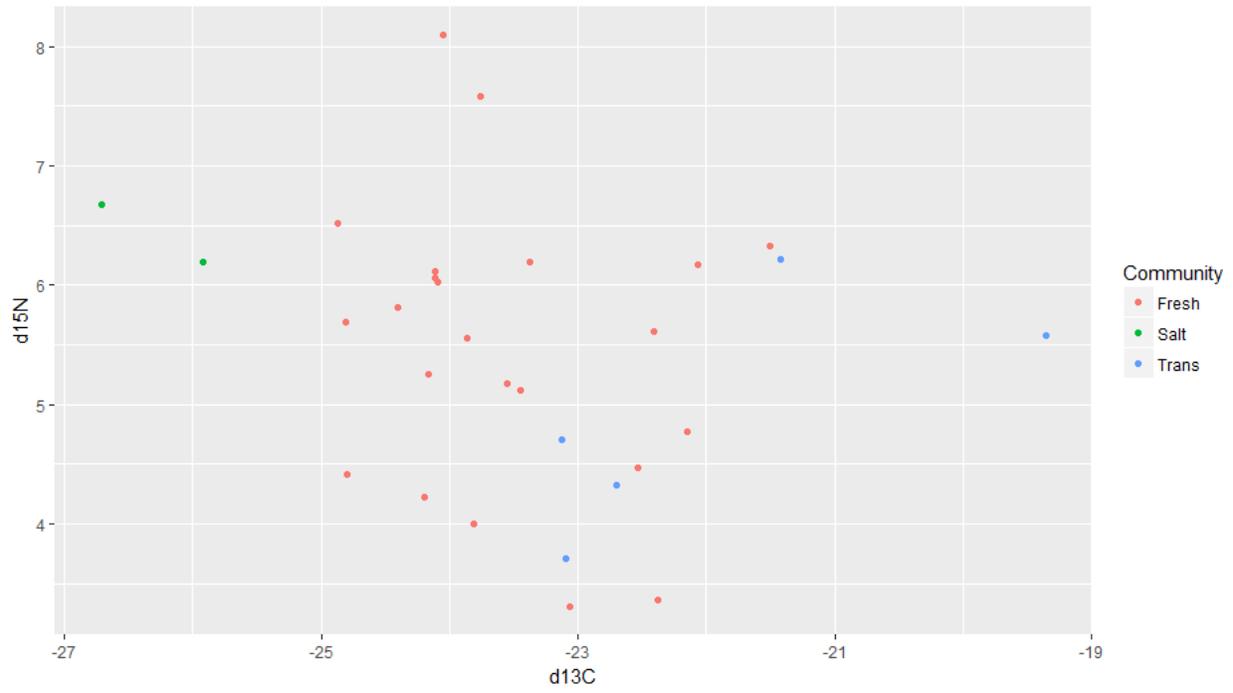
463

464 Fig. 1. Isotopic ratios of all samples (animal, hair, and plant) from both seasons.



465

466 Fig. 2. Hair sample isotopic ratios sorted by the season in which they were collected.



467

468 Fig. 3. Isotopic ratios of hair samples sorted by the vegetative community in which they were

469 captured.