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# Factors affecting individual foraging specialization and temporal diet stability across the range of a large “generalist” apex predator

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### Recommended Citation

Rosenblatt, A.E., Nifong, J.C., Heithaus, M.R. et al. *Oecologia* (2015) 178: 5. doi:10.1007/s00442-014-3201-6

This material is based upon work supported by the National Science Foundation through the Florida Coastal Everglades Long-Term Ecological Research program under Cooperative Agreements #DBI-0620409 and #DEB-9910514. Any opinions, findings, conclusions, or recommendations expressed in the material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation.

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2 **range of a large “generalist” apex predator**

3

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<sup>1</sup> Author Contributions: AER, JCN, MRH, and FJM conceived the idea for the study. AER, JCN, MSC, BMJ, RME, RAD, LJG, RHL, and JCL collected the data. AER and RAD analyzed the data. AER, JCN, MRH, and BRS wrote the manuscript; all other authors provided editorial advice.

22 **Abstract**

23 Individual niche specialization (INS) is increasingly recognized as an important  
24 component of ecological and evolutionary dynamics. However, most studies that have  
25 investigated INS have focused on the effects of niche width and inter- and intraspecific  
26 competition on INS in small-bodied species for short time periods, with less attention paid to  
27 INS in large-bodied reptilian predators and the effects of available prey types on INS. We  
28 investigated the prevalence, causes, and consequences of INS in foraging behaviors across  
29 different populations of American alligators (*Alligator mississippiensis*), the dominant aquatic  
30 apex predator across the southeast US, using stomach contents and stable isotopes. Gut contents  
31 revealed that over the short-term, although alligator populations occupied wide ranges of the INS  
32 spectrum, general patterns were apparent. Alligator populations inhabiting lakes exhibited lower  
33 INS than coastal populations, likely driven by variation in habitat type and available prey types.  
34 Stable isotopes revealed that over longer time spans alligators exhibited remarkably consistent  
35 use of variable mixtures of carbon pools (e.g., marine and freshwater food webs). We conclude  
36 that INS in large-bodied reptilian predator populations is likely affected by variation in available  
37 prey types and habitat heterogeneity, and that INS should be incorporated into management  
38 strategies to efficiently meet intended goals. Also, ecological models, which typically do not  
39 consider behavioral variability, should include INS to increase model realism and applicability.

40

41 Key words: American alligator, *Alligator mississippiensis*, stomach content analysis, stable  
42 isotope analysis, food web

43 **Introduction**

44 Intrapopulation foraging specialization can be attributed to differences between sexes  
45 (“ecological sexual dimorphism”; Temeles et al. 2000), morphological types (“resource  
46 polymorphisms”; Skulason and Smith 1995), and age groups (“ontogenetic niche shifts”; Polis  
47 1984). Increasingly, however, it is recognized that individuals within a population can exhibit  
48 considerable variation in trophic interactions that are not attributed to these factors, but instead to  
49 individual niche specialization (INS) that may be caused by differences in learning,  
50 morphological and physiological adaptive plasticity, and genetic and epigenetic expression (Dall  
51 et al. 2012). Individual niche specialization has important potential implications for evolutionary  
52 processes (Knudsen et al. 2010) and community and population dynamics (Bolnick et al. 2003;  
53 Dall et al. 2012). For example, some sea otter (*Enhydra lutris*) populations consist of individuals  
54 that exhibit extreme dietary specializations, possibly for their entire lives, likely resulting in low  
55 intraspecific competition and variable responses of individuals to food web perturbations (Estes  
56 et al. 2003).

57 A number of studies have examined various factors that affect the magnitude or  
58 occurrence of INS, including niche size (Bolnick et al. 2007; Woo et al. 2008; Araujo et al. 2009;  
59 Darimont et al. 2009), intraspecific competition (Estes et al. 2003; Tinker et al. 2008), and  
60 interspecific competition (Bolnick et al. 2010). However, another variable, prey community  
61 composition, has not been thoroughly examined as a potential factor affecting INS. Prey  
62 community composition is important to consider in the context of INS because for some species  
63 consumption of different prey types involves different handling times and attack success rates  
64 (Holling 1959; Kislalioglu and Gibson 1976). For example, if a predator population’s habitat  
65 contains abundant easy-capture prey (e.g., gastropods), then individuals in the population could

66 all consume large numbers of that prey group because of short handling times and high attack  
67 success rates. Such foraging behavior would cause each individual to exhibit dietary patterns  
68 very similar to conspecifics, resulting in low INS. In contrast, a habitat containing few easy-  
69 capture prey and different types of hard-capture prey (e.g., mammals and birds) could result in  
70 higher INS because the predators are less likely to all focus on the same elusive prey group and  
71 experience similar attack success rates (e.g., Baird et al. 1992). Killer whales (*Orcinus orca*) in  
72 the eastern North Pacific Ocean may fit such a pattern: two distinct groups of killer whales feed  
73 on different prey types, with “transients” primarily consuming pinnipeds and “residents”  
74 primarily consuming fish (Baird et al. 1992). For killer whales, pinnipeds are more difficult to  
75 capture and require more handling time than fish (Baird et al. 1992), and the resulting dietary  
76 specialization patterns of the two populations are highly divergent: residents display low dietary  
77 variability with prey killed by residents dominated by one genus of fish (*Oncorhynchus*) which  
78 makes up 98% of the diet, while transients display higher dietary variability with prey killed by  
79 transients distributed over 10 genera with harbor seals (*Phoca vitulina*) making up 55% of the  
80 diet (Ford et al. 1998).

81         The effects of prey community composition on INS are particularly important to  
82 investigate for large apex predators because they generally roam widely and can inhabit multiple  
83 ecosystems with different types of prey communities. Furthermore, large apex predator  
84 populations are generally declining globally (Ripple et al. 2014) and understanding INS patterns  
85 could be important for crafting appropriate conservation strategies (Bolnick et al. 2003). Some  
86 studies have documented the presence of INS in apex predators (Baird et al. 1992; Estes et al.  
87 2003; Tinker et al. 2008; Darimont et al. 2009; Matich et al. 2011; Thiemann et al. 2011), but  
88 few have addressed INS in one species across habitats with different prey community

89 compositions over large spatial scales. If there is variation in the strength of INS among different  
90 populations of the same top predator species across space and time (e.g., Baird et al. 1992), then  
91 the effects of those top predators on lower trophic levels could vary considerably within and  
92 among populations and their roles may differ markedly across ecosystems.

93         Here we investigate the prevalence and stability of INS as well as the effects of prey  
94 community composition on INS in a well-studied large apex predator: the American alligator  
95 (*Alligator mississippiensis*). Using complementary techniques, stomach contents analysis (SCA;  
96 provides short-term dietary data) and stable isotope analysis (SIA; provides long-term dietary  
97 data), we assess INS in alligators across their range and a variety of habitats. Alligators are  
98 excellent model “generalist” apex predators for such a study because: 1) their diets have been  
99 examined across their range repeatedly, 2) they inhabit every type of fresh and brackish water  
100 habitat across the southeastern US (Mazzotti and Brandt 1994), and 3) their diets at the  
101 population level are typically highly diverse. We hypothesized that alligator populations  
102 inhabiting lakes would display relatively low degrees of INS because of low habitat variability  
103 and prey communities containing many easy-capture prey (Darby et al. 2006). Conversely, we  
104 hypothesized that alligator populations in coastal habitats that have access to a variety of distinct  
105 habitat types (e.g., freshwater marshes, dynamic estuarine zones, marine areas) and to fewer  
106 easy-capture prey would exhibit higher degrees of INS.

107 **Materials and methods**

108 *Stomach contents collection and analyses*

109 We compiled alligator stomach contents data from seven published studies containing  
110 data collected from 1220 alligators between 1977 and 2004 and five new datasets collected from  
111 232 alligators between 2007 and 2012 (Table 1). The datasets included samples from a wide  
112 geographic range and many habitat types (freshwater lakes, mangrove rivers, salt marshes,  
113 barrier islands; Fig. 1). In some studies stomachs were sampled as part of state control programs  
114 (e.g., state-sanctioned hunting and nuisance alligator removal programs), while in others data  
115 were collected non-lethally using the hose-Heimlich technique (Table 1; Fitzgerald 1989). In  
116 studies that examined the technique's efficacy, 100% of ingested prey items were recovered from  
117 91% of the alligators tested (Fitzgerald 1989; Rice et al. 2005; Nifong et al. 2012); therefore, we  
118 assumed no sampling bias between studies that used lethal or non-lethal methods. Prey items  
119 found in the stomach contents were classified to the lowest possible taxon either immediately  
120 after collection or after preservation.

121 To assess the prevalence of INS in alligator populations we applied Roughgarden's  
122 (1972, 1979) concept of total niche width (TNW; full range of food resources used by a  
123 population), which is subdivided into a between-individual component (BIC; variance in food  
124 resource use between individuals) and within-individual component (WIC; variance in food  
125 resource use within individuals), such that  $TNW = BIC + WIC$ . If  $BIC > WIC$  for a given  
126 population, then the diets of individuals are more diverse in comparison to each other than they  
127 are diverse within each individual. We divided BIC by TNW to generate an index of  
128 specialization that varied between 0 and 1, where 0 = pure generalist population (individuals  
129 completely overlap with population's resource use) and 1 = pure specialist population



130 (individuals do not overlap at all with other individuals in the population). We chose to focus on  
131 the BIC/TNW index because it is simple to calculate and because other INS metrics generally  
132 produce similar results (Bolnick et al. 2002). Calculations of BIC/TNW are biased by the  
133 inclusion of individuals that only contain prey items from one prey group in their stomach  
134 (Bolnick et al. 2002), so we applied sorting rules to each dataset to limit bias in our INS results  
135 and produce more conservative BIC/TNW values (explanation in electronic supplemental  
136 materials).

137 Individual specialization metrics like BIC/TNW are difficult to compare across  
138 populations without accounting for variable numbers of available prey types across different  
139 habitats. Thus, to standardize our BIC/TNW values we converted them into adjusted  $E$  values  
140 ( $E_{adj}$ ; Araujo et al. 2011) using the equation

$$141 \quad E_{adj} = \frac{E_{obs} - E_{null}}{E_{max} - E_{null}}$$

142 where  $E_{obs}$  is the observed BIC/TNW value,  $E_{null}$  is the average BIC/TNW value generated by a  
143 Monte Carlo resampling procedure which assumes each individual samples randomly from a  
144 shared resource pool (explanation in electronic supplemental materials), and  $E_{max}$  is the  
145 maximum possible BIC/TNW value for a given population. The variable  $E_{max}$  can be calculated  
146 using the equation  $1-1/P$ , where  $P$  is the number of prey categories (families; see electronic  
147 supplemental materials) consumed by a predator population.

148 Since diet variation can be caused by sexual and ontogenetic differences, as well as  
149 inherent temporal and spatial prey variability, we needed to control for these potentially  
150 confounding factors before we could quantify INS. Therefore, we tested each stomach contents  
151 dataset to see if the datasets varied as a function of the variables capture season, capture year,  
152 capture location, size, and sex (Table S1) using principal component analysis and multivariate

153 analysis of variance (MANOVA; Araujo et al. 2007; explanation in electronic supplemental  
154 materials). If MANOVAs revealed that any of the independent variables were significant  
155 predictors of stomach contents variation in any given dataset, we divided the dataset into smaller  
156 subsets to remove the bias (e.g., splitting the dataset into male and female subsets to control for  
157 sex differences in diets). We chose the subsets of each dataset with sample sizes of at least 10  
158 individuals for BIC/TNW analysis using the program IndSpec 1.0 (Bolnick et al. 2002), then  
159 converted the BIC/TNW values into  $E_{adj}$  values. We used the program's Monte Carlo procedure  
160 to test the null hypothesis that any observed variation in diet was caused by individuals sampling  
161 randomly from a shared resource pool (Araujo et al. 2007; explanation in electronic  
162 supplemental materials).

163

#### 164 *Stable isotope collection and analyses*

165 For the purposes of INS analyses, SIA can be very useful because different tissues within  
166 the same consumer can incorporate isotopes from the diet over different time periods (i.e.,  
167 “turnover rates”; Dalerum and Angerbjorn 2005). Thus, multiple tissues collected from one  
168 individual can provide insight into the relative stability of dietary patterns – or at least basal  
169 carbon sources consumed – over multiple timescales. Although identifying specific consumed  
170 prey taxa with SIA is difficult for generalist carnivores with broad diets, SIA is still useful  
171 because values of  $\delta^{13}\text{C}$  are indicative of the origin of a consumer's nutrients (Fry 2006).

172 Tissue-specific turnover rates can vary widely between species (Dalerum and Angerbjorn  
173 2005). A diet-switch study of juvenile alligators (Rosenblatt and Heithaus 2013) revealed that the  
174 approximate complete turnover time of alligator plasma for  $\delta^{13}\text{C}$  (252 days) was roughly half  
175 that of red blood cells (RBCs; 566 days). Therefore, if  $\delta^{13}\text{C}$  values for an alligator were similar

176 across these tissue types it would suggest that the mixture of carbon pools used across an eight  
177 month period prior to sample collection is similar to that used across a 19-month period prior to  
178 sample collection. Differing  $\delta^{13}\text{C}$  values would indicate shifts in the relative contributions of  
179 different carbon pools across these timescales. For our analyses we used stable isotope data from  
180 plasma and RBC samples from 214 alligators collected between 2008 and 2012 from six sites  
181 (Table 1; see Rosenblatt and Heithaus (2013) for sample collection procedures and the electronic  
182 supplemental materials for laboratory analysis procedures).

183 Before assessing the prevalence of INS in the alligator populations using SIA we needed  
184 to remove the possibility that our results were affected by variable fractionation factors between  
185 the two tissues (Dalerum and Angerbjorn 2005). Therefore, we subtracted experimentally  
186 determined fractionation values (isotopic differences between tissues and diet) for each alligator  
187 tissue (+0.35‰ for plasma  $\delta^{15}\text{N}$ , -0.04‰ for plasma  $\delta^{13}\text{C}$ , +0.95‰ for RBC  $\delta^{15}\text{N}$ , and +0.03‰  
188 for RBC  $\delta^{13}\text{C}$ ; Rosenblatt and Heithaus 2013) from the  $\delta$  values for each tissue. Then,  
189 MANOVAs were used to determine if the stable isotope datasets were significantly affected by  
190 the variables capture season, capture location, size, or sex. We only focused on the  $\delta^{13}\text{C}$  values  
191 of the two tissues as the dependent variables because they contain information about nutrient  
192 origins. After controlling for possible confounding variables and the potential effects of  
193 fractionation factors, we determined correlation coefficients for each dataset to see if the  
194 relationships between the  $\delta^{13}\text{C}$  values of plasma and RBCs were linear and positive (i.e.,  
195 exhibited correlation coefficients close to one). We then employed linear regression to further  
196 examine the relationship between the  $\delta^{13}\text{C}$  values of plasma and RBCs. If individual alligators  
197 exhibited stable foraging patterns over the long time periods represented by the two tissues, we  
198 would expect the  $\delta^{13}\text{C}$  values of plasma and RBCs to be highly correlated, with linear regression

199 best-fit lines characterized by high  $R^2$  values and slopes close to one. Conversely, if alligators  
200 exhibited more variable foraging patterns we would expect best-fit lines characterized by low  $R^2$   
201 values and slopes farther away from one. All statistical analyses were performed in SPSS 17.0  
202 (IBM, Armonk, NY, USA) and SigmaPlot 11.0 (Systat, Chicago, IL).

203 **Results**

204 *Stomach contents*

205         The alligators in this study consumed a diverse array of prey. The number of prey  
206 families consumed per study ranged from 11 to 38 (mean =  $23.1 \pm 9.2$  SD) and the mean number  
207 of individual prey items consumed per alligator per study ranged from 4.5 to 34.8 (mean =  $16.5 \pm$   
208  $11.3$  SD). Prey included crustaceans, mollusks, fishes, amphibians, reptiles, mammals, birds,  
209 aquatic and terrestrial insects, and seeds (Table S2). Alligators with empty stomachs made up  
210 6.1% (N = 89) of all the individuals (mean per study =  $7.3\% \pm 6.7$  SD), and 27.8% (N = 403) of  
211 alligator stomachs contained only 1 prey item or 2 prey items in the same prey category (mean  
212 per study =  $26.3\% \pm 14.5$  SD). Therefore, according to our sorting rules, we removed 33.9% of  
213 the alligators from further analyses, leaving 960 individuals.

214         The PCA-MANOVA analyses revealed that for most of the datasets (7 out of 12 total)  
215 there existed differences in diet separate from INS (Table S1). Capture location was a significant  
216 predictor of dietary patterns in 60% (3 of 5) of lake studies and 67% (2 of 3) of estuarine  
217 habitats. Capture season was a significant predictor of dietary patterns in all three of the studies  
218 in which it was included and capture year was a significant predictor in two (67%) of the studies.  
219 Alligator size was a significant predictor of dietary patterns in 58% of the studies (7 of 12)  
220 whereas sex was a significant predictor in two of the nine (22%) studies in which it was  
221 included.

222         After subdividing each dataset to control for significant predictor variables, the resulting  
223 Shark River dataset was removed from further analyses because it was heavily skewed by two  
224 individuals that each consumed thousands of anchovies (Engraulidae). The remaining 28  
225 populations and sub-populations only included 23 monophagous individuals between them and

226 produced  $E_{adj}$  specialization values that varied widely, with a minimum of 0.03 and a maximum  
227 of 0.74 (mean =  $0.39 \pm 0.19$  SD; Table 2). The Monte Carlo simulations revealed that despite the  
228 wide range of observed BIC/TNW values, all but one population exhibited significantly greater  
229 specialization than predicted by chance (Table 2). The  $E_{adj}$  values were not affected by sample  
230 size (linear regression:  $R^2 = 0.007$ ,  $P = 0.7$ ), but the  $E_{adj}$  values were significantly different  
231 between habitat types (t-test:  $t_{26} = -2.7$ ,  $P = 0.01$ ), with populations from lakes exhibiting lower  
232 values (mean =  $0.35 \pm 0.17$  SD) than populations from coastal habitats (mean =  $0.58 \pm 0.14$  SD).

233 Mollusks were one of the most frequently consumed prey groups across the populations  
234 and there was a significant negative relationship between the  $E_{adj}$  values of a population and the  
235 number of mollusks consumed as a percentage of the population's total diet ( $R^2 = 0.3$ ,  $P = 0.003$ ;  
236 Fig. 2). There were also striking differences in mollusk consumption between lake and coastal  
237 populations: lake populations consumed significantly more mollusks per individual (mean =  $9.0$   
238  $\pm 12.0$  SD) than coastal populations (mean =  $0.2 \pm 0.1$  SD; Mann-Whitney U test:  $U = 1$ ,  $P <$   
239  $0.001$ ) and significantly more mollusks as a percentage of the population's total diet (mean =  
240  $51.0\% \pm 26.0$  SD) than coastal populations (mean =  $1.5\% \pm 2$  SD;  $U = 1$ ,  $P < 0.001$ ). Lastly, our  
241 analyses indicated lake alligator populations used fewer potential prey categories present in their  
242 habitat ( $48\% \pm 21$  SD) when compared to coastal populations ( $70\% \pm 35$  SD), though this  
243 difference was not statistically significant (Mann-Whitney U test:  $U = 37$ ,  $P = 0.2$ ).

244

#### 245 *Stable isotopes*

246 The fractionation-corrected  $\delta^{13}\text{C}$  values from both plasma and RBCs varied in the stable  
247 isotope datasets with five of the six populations exhibiting wide  $\delta^{13}\text{C}$  ranges (Table 3). We did  
248 not use the Lake Woodruff isotopes in our analyses because the  $\delta^{13}\text{C}$  ranges for both plasma and

249 RBCs (Table 3) were too small to confidently estimate INS in this population. The large  $\delta^{13}\text{C}$   
250 ranges in the other alligator populations are indicative of the large ranges in  $\delta^{13}\text{C}$  values of  
251 resource pools available to the alligator populations in each habitat (Peterson and Howarth 1987;  
252 Gu et al. 1997; Rosenblatt and Heithaus 2011; Adams and Paperno 2012) and that individuals  
253 within these populations display considerable variation in the proportions of food they consume  
254 from these different resource pools over the timescales of plasma and RBC turnover.

255 Capture location (freshwater/intermediate/marine habitats) was a significant predictor of  
256  $\delta^{13}\text{C}$  values in two of the three estuarine studies (Table S1). Also, sex had a significant effect on  
257  $\delta^{13}\text{C}$  values in the Lake Apopka study so only males were included in analyses (Table S1). In  
258 addition, size had a significant effect on  $\delta^{13}\text{C}$  values in the Sapelo Island study (Table S1), with  
259 the two smaller alligator size classes displaying much lower  $\delta^{13}\text{C}$  values than the two larger size  
260 classes. For eight out of nine subpopulations from the five isotope datasets plasma and RBC  $\delta^{13}\text{C}$   
261 values exhibited tight linear relationships, with correlation coefficient (Pearson's  $r$ ) values  
262 ranging from 0.88 to 0.99 (mean =  $0.96 \pm 0.04$  SD). The Guana River population was the lone  
263 outlier with a Pearson's  $r$  value of 0.52. The results of linear regression also showed that the  $\delta^{13}\text{C}$   
264 values of the two tissues were highly correlated, with  $R^2$  values ranging from 0.77 to 0.99 (mean  
265 =  $0.92 \pm 0.07$  SD, all  $P < 0.001$ ) and with slopes very close to 1, ranging from 0.79 to 1.08  
266 (mean =  $0.96 \pm 0.09$  SD; Fig. 3). Indeed, seven of the eight slope values did not differ  
267 significantly from a slope of 1 (all  $P > 0.1$ ). The lone outlier again was the Guana River  
268 population, which also showed a positive relationship but a lower  $R^2$  value (0.28) and slope  
269 (0.49).

## 270 **Discussion**

271 Our results show that species thought to be dietary generalists and that exhibit broad  
272 population level diets can actually specialize at the individual level. Stomach contents analysis  
273 revealed that alligator populations exhibit different short-term dietary patterns, ranging from  
274 generalized to more specialized populations. We also found the strength of short-term INS was  
275 context dependent, with populations from lakes containing many easy-capture prey exhibiting  
276 lower INS than populations from other habitats containing fewer easy-capture prey. In addition,  
277 SIA revealed long-term stability in the use of different carbon pools by individual alligators  
278 despite large differences between the  $\delta^{13}\text{C}$  values of those carbon pools: eight out of nine  
279 populations we studied from both lake and coastal habitats contained individuals with  
280 remarkably consistent  $\delta^{13}\text{C}$  values over moderate to long time spans, indicating that alligators  
281 generally maintain the same foraging patterns through time regardless of habitat type.  
282 Importantly, INS existed in addition to the dietary variation caused by differences between sexes,  
283 life stages, seasons, years, and locations.

284 Consistent with our hypotheses, our findings suggest that one of the main drivers of INS,  
285 at least in the short-term, is habitat heterogeneity and prey community composition. Lower  $E_{adj}$   
286 values in alligator populations inhabiting lakes could be a consequence of low habitat variation  
287 in lakes and their well-defined boundaries. For example, Lake Apopka in central Florida, whose  
288 alligator population was sampled several times across our datasets, has been a shallow,  
289 homogenous, turbid, algal-dominated lake lacking a diverse fishery since 1947 (Bachmann et al.  
290 1999). In contrast, the estuarine habitats sampled across our datasets contain a diversity of  
291 aquatic habitats (freshwater, estuarine, marine) and have diffuse boundaries, thus potentially  
292 allowing for greater movement of alligators and greater ingress of possible prey taxa. In fact,



293 movement studies indicate that alligators inhabiting lakes move shorter distances and occupy  
294 smaller ranges than alligators in coastal habitats, and lake alligators largely restrict themselves to  
295 littoral areas (Goodwin and Marion 1979; Rosenblatt et al. 2013). Together, these observations  
296 suggest that lake-bound alligators have access to less distinct habitat types and prey groups than  
297 coastal populations. Consistent with this hypothesis, our analyses indicated lake alligator  
298 populations used fewer prey categories present in their habitat when compared to non-lake  
299 populations, though this result was not statistically significant.

300         Though the specific effects of habitat heterogeneity on INS have not been examined  
301 extensively, our findings agree with the few studies that have been done. For example, in a study  
302 of wolf (*Canis lupus*) feeding patterns in coastal British Columbia researchers found that wolves  
303 inhabiting island habitats exhibited relatively more among-individual dietary variation than  
304 mainland wolves. This difference was at least partially attributable to the fact that island wolves  
305 had access to multiple food webs (terrestrial and marine) embedded in a spatially heterogenous  
306 area while mainland wolves only used one food web (terrestrial) in a more spatially homogenous  
307 area (Darimont et al. 2009). Furthermore, trophic niche width of a population, a factor that can  
308 affect INS, also can decrease as habitat heterogeneity decreases (Layman et al. 2007). These  
309 studies broadly agree with our results, but more research on the effects of habitat heterogeneity  
310 on INS across a greater diversity of species and habitats is needed to confirm our findings.

311         Our results further suggest that prey community composition can drive short-term INS  
312 because the  $E_{adj}$  values were negatively correlated with the number of mollusks consumed by a  
313 population as a percentage of the whole diet. We hypothesize that the presence of abundant easy-  
314 capture prey like mollusks in certain habitats may allow the majority of alligators in those  
315 habitats to take frequent advantage of a resource so easily found and consumed. However, when

316 mollusks are not as abundant alligators must pursue more mobile prey that are harder to capture.  
317 These contrasting contexts would make each individual's short-term diet in mollusk-rich habitats  
318 (i.e., lakes; Darby et al. 2006) more similar to conspecifics, thereby decreasing INS, but more  
319 different from conspecifics in habitats containing less abundant mollusks, thereby increasing INS  
320 (e.g., Baird et al. 1992; Tinker et al. 2008). In the latter context dietary variation between  
321 individuals could be caused by resource patchiness rather than behavioral specialization, but  
322 available evidence suggests that alligators do not move randomly through their environment  
323 because individuals visit the same foraging areas over multiple years (Rosenblatt and Heithaus  
324 2011; Rosenblatt et al. 2013). Although individuals may return to similar locations for periods of  
325 time, their foraging trips take them to areas with prey supported by different carbon sources (e.g.  
326 marine versus freshwater production). Thus, INS in habitats dominated by more mobile prey  
327 could be caused by fine-scale associations between individual alligators and specific areas or by  
328 individuals learning to eat different prey.

329         The effects of prey capture difficulty on INS have not been extensively studied, but our  
330 results agree with those from killer whales which show that as prey capture difficulty increases  
331 INS increases as well (Baird et al. 1992; Ford et al. 1998). However, a more recent study on  
332 much smaller predators (wasps; Crabronidae and Sphecidae) showed the opposite effect of prey  
333 capture difficulty on INS (Polidori et al. 2013). These incongruent results may be the result of  
334 different habitat types (aquatic vs. terrestrial), differences in prey modes of movement (flying vs.  
335 swimming), or differences in scale. Regardless of the cause of the differences it is clear that the  
336 effects of prey capture difficulty can affect INS and more research is needed to identify the  
337 mechanisms involved.

338           Stomach contents analysis has specific drawbacks pertaining to INS. For example, SCA  
339 can be biased by variable digestive rates of different prey items. Prey with indigestible parts  
340 (e.g., arthropods with chitinous exoskeletons, turtles, mollusks) may become over-represented in  
341 the diet because they remain in the stomach longer than soft-bodied vertebrate prey (Garnett  
342 1985; Janes and Gutzke 2002; Nifong et al. 2012). This factor can cause some prey to appear  
343 more frequently and in higher numbers in stomachs, which may bias dietary analyses. However,  
344 most of the prey groups consumed by alligators in our synthesis have at least one indigestible  
345 part (e.g., mammal hair, bird feathers, crustacean exoskeletons, snail shells) which means  
346 variable digestive rates likely did not have a large effect on our results, with the exception of a  
347 possible underestimation of amphibians and fishes (Table S2).

348           There are three additional caveats associated with our stomach contents analyses. First,  
349 we are confident that alligators exhibit non-random foraging behaviors, thereby violating one of  
350 the assumptions of the Monte Carlo null hypothesis testing procedure. This means that the  
351 statistical significance of our INS results is not conservative and should be viewed with caution.  
352 Second, intraspecific competition is known to affect INS (Estes et al. 2003; Tinker et al. 2008)  
353 and to account for this factor we would need to include alligator density and prey density in our  
354 analyses. Unfortunately, both of these forms of data were not available for any of the locations  
355 we included in our analyses, so there is a possibility that our INS results were also affected by  
356 differences in intraspecific competition between habitat types. Third, we grouped alligator prey  
357 by family because we assumed that alligators do not discriminate between prey on the species or  
358 even genus level. If alligators do actually show preferences on the species or genus level, then  
359 our INS estimates would be conservative and real alligator INS values may be higher, i.e.  
360 alligator populations may be more specialized. In contrast, if the opposite were true and

361 alligators do not discriminate between prey even on the family level, then alligator populations  
362 may actually be less specialized.

363 SIA revealed that alligators generally exhibited highly consistent use of different carbon  
364 pools across longer time frames. The consistent  $\delta^{13}\text{C}$  values we observed across tissues could  
365 have been caused by specialization on specific prey but could also be attributed to consistent use  
366 of specific habitats and movement patterns. We hypothesize that the latter explanation is more  
367 likely, i.e. that alligators specialize in certain behavioral patterns, like specific foraging and  
368 movement tactics. This possibility was partially accounted for in our study by separating  
369 analyses for individuals captured in different habitats, but because of their high mobility  
370 alligators captured in the same habitat still could move across the landscape in different ways.  
371 Our hypothesis is supported by a previous study of alligator movement patterns in the Shark  
372 River where alligators exhibited temporally stable variation in movement patterns (Rosenblatt  
373 and Heithaus 2011; Rosenblatt et al. 2013): half of the alligators regularly commuted between  
374 freshwater/estuarine and marine habitats and the stable isotope values of their skin indicated that  
375 they were consistently feeding in two different food webs, whereas other alligators limited their  
376 movements and feeding strictly to freshwater/estuarine habitats. Similar patterns appear to occur  
377 in sea turtles, although on a different time scale, in that individual turtles will use consistent  
378 “corridors” to move between nesting and foraging areas and will return to the same foraging  
379 areas repeatedly, or individuals from the same nesting populations may be either coastal or  
380 pelagic in their foraging habitats (see Heithaus 2013 for a review). Our study and others point to  
381 the difficulties in using SIA to infer INS behaviors as a standalone data source when turnover  
382 rates of even “fast” tissues are long, as in most reptiles (Rosenblatt and Heithaus 2013), because  
383 in such situations SIA fails to capture short-term dietary choices. Therefore, we echo previous

384 studies in suggesting that INS studies should combine isotope data with other behavioral data  
385 where possible. We should also note that the turnover rate of alligator plasma is almost 50% of  
386 the turnover rate for alligator RBCs, thus inherently biasing our analyses towards strong  
387 correlations between the  $\delta^{13}\text{C}$  values of the two tissues. However, despite this methodological  
388 artifact we are confident in our results because of the remarkable strength of the correlations  
389 across almost every alligator population we sampled.

390         Many current ecosystem management and conservation strategies assume that all apex  
391 predators in a population will have similar effects on prey populations. However, if behaviors  
392 vary consistently across individuals, as our study and those of other taxa (Bolnick et al. 2003)  
393 suggest, then one-size-fits-all conservation and management strategies may have unintended  
394 consequences in many systems. For example, the Shark River is part of the Everglades which is  
395 an ecosystem currently undergoing large-scale restoration (Doren et al. 2009). Restoration  
396 activities are expected to bring more freshwater to the area, thereby decreasing salinity and  
397 potentially increasing habitat quality for alligators that are dependent on freshwater (Mazzotti  
398 and Brandt 1994). Since many of the alligators in this system appear to specialize in exploiting  
399 the marine food web seasonally (Rosenblatt and Heithaus 2011), increased freshwater flow may  
400 positively impact this group by allowing them to access marine resources for a larger portion of  
401 each year (though the distribution of marine prey may change as well). However, individuals that  
402 do not currently take advantage of marine resources may not experience the same future benefits.  
403 In addition, the spatial scale of alligator movements, and therefore potential coupling of food  
404 webs and nutrient transport (Rosenblatt and Heithaus 2011), likely will change. As freshwater  
405 moves seaward, any individuals exploiting marine food webs will not need to move as far  
406 upstream for osmoregulation. Similarly, in northern Kenya, African wild dog (*Lycaon pictus*)

407 populations outside of protected areas exhibit specialized feeding on smaller prey than  
408 populations inside protected areas (Woodroffe et al. 2007). Thus, if wild dog conservation efforts  
409 were solely aimed at bolstering large prey populations some wild dogs may see no benefit unless  
410 their feeding patterns are very plastic. Different restoration and conservation scenarios, therefore,  
411 may differentially benefit subsets of apex predator populations. As a result, restoration and  
412 conservation actions may not achieve their intended goals if individual behavioral specialization  
413 is not explicitly considered during the planning process.

414         Our results also have important implications for food web theory and ecosystem models.  
415 Theoretical analyses have shown that top predators that couple different food webs through their  
416 foraging and movement behaviors contribute both local and non-local stability to the food webs  
417 (Rooney et al. 2006), but such models treat individuals in predator populations as behaviorally  
418 homogenous. By incorporating behaviorally heterogenous predator populations into food web  
419 and ecosystem models, realism of theoretical analyses and scenarios will increase (Quevedo et  
420 al. 2009). These next-generation models may reveal insights into the potentially nuanced roles of  
421 top predators in ecosystems and allow for the development of additional testable hypotheses.

422         Ultimately, our research shows that INS in large apex predators can vary substantially  
423 among populations and the degree of inter-individual variation is likely affected by habitat type  
424 and prey community composition. Future research could make valuable contributions to our  
425 understanding of INS by investigating the relative effects of prey community composition, niche  
426 width, and inter- and intraspecific competition across a wider range of taxonomic groups, body  
427 sizes, and trophic levels. In the context of INS in large apex predators, it remains to be seen how  
428 subpopulations exhibiting different behaviors will respond to specific ecosystem conservation  
429 and management scenarios, but it is clear that INS needs to be explicitly considered in such plans

430 as well as in food web models.

431 **Acknowledgements**

432           We thank Michael Delany, Steven Gabrey, and Amanda Rice for generously allowing us  
433 to use their alligator stomach contents data. This research was made possible by funding from the  
434 National Science Foundation through the Florida Coastal Everglades Long-Term Ecological  
435 Research program under Grant No. DBI-0620409 and from the National Oceanic and  
436 Atmospheric Administration under Award No. NA10NOS4200022 (09102903). Additional  
437 funding was provided by Florida International University (FIU) and the University of Florida  
438 (UF). AER was supported by an FIU Dissertation Year Fellowship during manuscript  
439 preparation. All animal care and use was performed in accordance with the UF Institutional  
440 Animal Care and Use Committee (IACUC) under Protocol No. 201005071, the FIU IACUC  
441 under Protocol No. 09-015 and 09-013, and the Kennedy Space Center IACUC under Protocol  
442 No. GRD-06-044. All field collections were performed under FFWCC Scientific Collecting  
443 Permit No. SPGS-10-44R and SPGS-10-43, Georgia Department of Natural Resources Scientific  
444 Collecting Permit No. 29-WBH-10-33, and Everglades National Park Permit No. 0024, 0025,  
445 and 0031. We thank all the volunteers who assisted with field work and data collection,  
446 especially Phil Matich, Kirk Gastrich, Katy Cameron, Greg Mineau, and Derek Burkholder. Use  
447 of trade, product, or firm names does not imply endorsement by the U.S. Government or the  
448 authors. All work carried out in this study comply with the current laws of the USA. We declare  
449 that we have no conflict of interest.



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565  
566

Table 1 Summary information for the American alligator stomach contents and stable isotope studies used in analyses.

<b>Data source</b>	<b>Locations</b>	<b>Habitat type</b>	<b>Duration</b>	<b>Collection method</b>	<b>N</b>
<b>Stomach contents</b>					
Delany and Abercrombie 1986	Orange, Lochloosa, & Newnans Lakes, FL	Lake	1981-1983	Hunter harvested alligators	349
Delany et al. 1988	Duval, St. Johns, Alachua, Marion, Citrus, & Lake counties, FL	Lake	1977	Sacrificed nuisance alligators	78
Delany 1990	Orange Lake, FL	Lake	1986	Sacrificed alligators	77
Elsey et al. 1992	Marsh Island, LA	Island	1991	Hunter harvested alligators	101
Delany et al. 1999	Rodman, George, Hancock, & Trafford Lakes, FL	Lake	1985	Hunter harvested alligators	231
Rice et al. 2007	Apopka, Griffin, & Woodruff Lakes, FL	Lake	2001-2003	Hose-Heimlich stomach flushing	172
Gabrey 2010	Lafourche, Terrebonne, Cameron, Vermilion, & St. Charles parishes, LA	Marsh	2002-2004	Hunter harvested alligators	212
This study	Apopka & Woodruff Lakes, FL	Lake	2010	Hose-Heimlich stomach flushing and necropsies	29
	Merritt Island, FL	Island	2010	Hose-Heimlich stomach flushing and necropsies	10
	Shark River, FL	Estuary	2009-2011	Hose-Heimlich stomach flushing	54
	Guana River, FL	Estuary	2011-2012	Hose-Heimlich stomach flushing	40
J. Nifong (unpub. data)	Sapelo Island, GA	Island	2007-2010	Hose-Heimlich stomach flushing	99
<b>Stable isotopes</b>					
This study	Apopka & Woodruff Lakes, FL	Lake	2010	NA	29
	Merritt Island, FL	Island	2010	NA	10
	Shark River, FL	Estuary	2008-2011	NA	79
	Guana River, FL	Estuary	2011-2012	NA	40
J. Nifong (unpub. data)	Sapelo Island, GA	Island	2009-2010	NA	56

567

568 Table 2 Results of American alligator stomach contents specialization analyses. BIC/TNW = Between Individual Component/Total Niche Width  
 569 (observed), BIC/TNW MC = mean value generated by Monte Carlo simulations, TL = Total Length of alligators, SVL = Snout-Vent Length of  
 570 alligators.  
 571

Data source	Location	Sample date	Sex	Size (TL; cm)	N	BIC/TNW (E <sub>obs</sub> )	BIC/TNW MC (E <sub>null</sub> )	E <sub>max</sub> (prey categories)	E <sub>adjusted</sub>
Delany and Abercrombie 1986	Orange Lake, FL	Fall 1983	M, F	200-250	22	0.71**	0.20	0.94 (17)	0.69
	Lochloosa Lake, FL	Fall 1981	M, F	150-200	10	0.68**	0.20	0.9 (10)	0.69
	Orange Lake, FL	Fall 1982	M, F	150-200	22	0.58**	0.38	0.93 (14)	0.36
	Orange Lake, FL	Fall 1981	M, F	250-300	10	0.55**	0.40	0.94 (16)	0.28
	Orange Lake, FL	Fall 1983	M, F	100-150	12	0.52**	0.28	0.93 (14)	0.37
	Orange Lake, FL	Fall 1982	M, F	200-250	19	0.52**	0.42	0.93 (15)	0.19
	Orange Lake, FL	Fall 1982	M, F	100-150	13	0.52**	0.38	0.92 (13)	0.26
	Orange Lake, FL	Fall 1983	M, F	250-300	13	0.51**	0.32	0.92 (13)	0.32
	Orange Lake, FL	Fall 1982	M, F	250-300	10	0.48**	0.35	0.88 (8)	0.25
	Newnan's Lake, FL	Fall 1983	M	300-350	15	0.48**	0.32	0.91 (11)	0.27
Newnan's Lake, FL	Fall 1983	M, F	200-250	11	0.43**	0.22	0.9 (10)	0.31	
Delany et al. 1988	Griffin & Tsala Apopka Lakes, FL	Summer 1977	M, F	100-350	27	0.58	0.57	0.93 (14)	0.03
Delany 1990	Orange Lake, FL	Fall 1986	NA	50-100	27	0.56**	0.25	0.91 (11)	0.47
	Orange Lake, FL	Fall 1986	NA	0-50	27	0.54**	0.24	0.9 (10)	0.45
	Orange Lake, FL	Fall 1986	NA	100-150	13	0.48**	0.18	0.92 (13)	0.4
Elsley et al. 1992	Marsh Island, LA	Summer 1991	M, F	100-200	81	0.57**	0.22	0.95 (22)	0.48
Delany et al. 1999	Rodman Lake, FL	Summer 1985	M	250-300	15	0.45**	0.11	0.94 (16)	0.41
	George Lake, FL	Summer 1985	M, F	150-200	18	0.46**	0.18	0.92 (12)	0.38
	George Lake, FL	Summer 1985	M, F	100-150	12	0.44**	0.16	0.89 (9)	0.38
	Rodman Lake, FL	Summer 1985	M, F	200-250	11	0.33**	0.08	0.89 (9)	0.31
	George Lake, FL	Summer 1985	M, F	200-250	10	0.55**	0.44	0.89 (9)	0.25
	Rodman Lake, FL	Summer 1985	M	300-350	10	0.24**	0.14	0.91 (11)	0.13
Rice et al. 2007	Woodruff Lake, FL	Fall 2002	M, F	200-250	12	0.70**	0.10	0.92 (12)	0.73
Gabrey 2010	Freshwater marsh, LA	Fall 2004	M	75-100 (SVL)	15	0.79**	0.57	0.9 (10)	0.67
This study	Merritt Island, FL	Spring 2010	M	250-350	7	0.69**	0.07	0.91 (11)	0.74
	Guana River, FL	Summer 2011-2012	M, F	50-250	30	0.64**	0.11	0.95 (21)	0.63
	Apopka & Woodruff Lakes, FL	Spring 2010	M, F	200-350	20	0.47**	0.35	0.92 (13)	0.21
J. Nifong (unpub. data)	Sapelo Island, GA	Spring 2008	M	50-100	10	0.50**	0.29	0.83 (6)	0.39

572 \*\* $P < 0.001$  (Monte Carlo bootstraps, 500 simulations)

573 All others,  $P = 0.3$

574 Table 3 Summary of fractionation-corrected  $\delta^{13}\text{C}$  ranges for plasma and red blood cells (RBC) for each American alligator population used in the  
575 study.

Location	Min plasma $\delta^{13}\text{C}$ (‰)	Max plasma $\delta^{13}\text{C}$ (‰)	Plasma $\delta^{13}\text{C}$ mean $\pm$ SD (‰)	Min RBC $\delta^{13}\text{C}$ (‰)	Max RBC $\delta^{13}\text{C}$ (‰)	RBC $\delta^{13}\text{C}$ mean $\pm$ SD (‰)
Sapelo Island, GA	-29.4	-15.3	-21.5 $\pm$ 4.5	-28.0	-14.0	-21.0 $\pm$ 4.5
Lake Apopka, FL	-25.9	-11.9	-16.5 $\pm$ 4.9	-25.2	-12.1	-16.3 $\pm$ 4.8
Shark River, FL	-30.3	-19.2	-26.2 $\pm$ 2.1	-28.7	-21.1	-26.0 $\pm$ 1.7
Guana River, FL	-24.6	-18.0	-20.8 $\pm$ 1.3	-25.0	-18.0	-21.1 $\pm$ 1.4
Merritt Island, FL	-22.8	-16.8	-19.0 $\pm$ 2.0	-23.2	-15.2	-18.0 $\pm$ 2.3
Lake Woodruff, FL	-26.4	-24.4	-25.4 $\pm$ 0.6	-26.0	-23.3	-24.8 $\pm$ 0.7

576

577



578 **Figure captions**

579

580 **Fig. 1** Map of alligator sampling locations used for diet specialization analyses. Circles = lakes,  
581 squares = islands, triangles = marshes, and diamonds = rivers/estuaries. Black shapes represent  
582 locations where only stomach contents were collected and gray shapes represent sites where both  
583 stomach contents and tissues for stable isotope analysis were collected

584

585 **Fig. 2** Specialization values ( $E_{adj}$ ) of different American alligator populations as predicted by  
586 mollusk consumption (total number of mollusks consumed by population divided by total  
587 number of all prey items consumed by population). Black line is linear regression trend line

588

589 **Fig. 3** Linear regression plots depicting relationships between alligator plasma  $\delta^{13}\text{C}$  values and  
590 red blood cell  $\delta^{13}\text{C}$  values. **a** Lake Apopka, FL (males, lake habitat, 250-400 cm total length  
591 (TL)), **b** Sapelo Island, GA (males and females, marine habitat, 100-150 cm TL), **c** Sapelo  
592 Island, GA (males, marine habitat, 50-100 cm TL), **d** Shark River, FL (males and females,  
593 estuarine habitat, 150-300 cm TL). All  $P < 0.001$ . Note different scales on axes