2-3-2015

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

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[1] 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.

Abstract

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

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

Introduction

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

A number of studies have examined various factors that affect the magnitude or occurrence of INS, including niche size (Bolnick et al. 2007; Woo et al. 2008; Araujo et al. 2009; Darimont et al. 2009), intraspecific competition (Estes et al. 2003; Tinker et al. 2008), and interspecific competition (Bolnick et al. 2010). However, another variable, prey community composition, has not been thoroughly examined as a potential factor affecting INS. Prey community composition is important to consider in the context of INS because for some species consumption of different prey types involves different handling times and attack success rates (Holling 1959; Kislalioglu and Gibson 1976). For example, if a predator population’s habitat contains abundant easy-capture prey (e.g., gastropods), then individuals in the population could all consume large numbers of that prey group because of short handling times and high attack success rates. Such foraging behavior would cause each individual to exhibit dietary patterns very similar to conspecifics, resulting in low INS. In contrast, a habitat containing few easy-capture prey and different types of hard-capture prey (e.g., mammals and birds) could result in higher INS because the predators are less likely to all focus on the same elusive prey group and experience similar attack success rates (e.g., Baird et al. 1992). Killer whales (*Orcinus orca*) in the eastern North Pacific Ocean may fit such a pattern: two distinct groups of killer whales feed on different prey types, with “transients” primarily consuming pinnipeds and “residents” primarily consuming fish (Baird et al. 1992). For killer whales, pinnipeds are more difficult to capture and require more handling time than fish (Baird et al. 1992), and the resulting dietary specialization patterns of the two populations are highly divergent: residents display low dietary variability with prey killed by residents dominated by one genus of fish (*Oncorhynchus*) which makes up 98% of the diet, while transients display higher dietary variability with prey killed by transients distributed over 10 genera with harbor seals (*Phoca vitulina*) making up 55% of the diet (Ford et al. 1998).

The effects of prey community composition on INS are particularly important to investigate for large apex predators because they generally roam widely and can inhabit multiple ecosystems with different types of prey communities. Furthermore, large apex predator populations are generally declining globally (Ripple et al. 2014) and understanding INS patterns could be important for crafting appropriate conservation strategies (Bolnick et al. 2003). Some studies have documented the presence of INS in apex predators (Baird et al. 1992; Estes et al. 2003; Tinker et al. 2008; Darimont et al. 2009; Matich et al. 2011; Thiemann et al. 2011), but few have addressed INS in one species across habitats with different prey community compositions over large spatial scales. If there is variation in the strength of INS among different populations of the same top predator species across space and time (e.g., Baird et al. 1992), then the effects of those top predators on lower trophic levels could vary considerably within and among populations and their roles may differ markedly across ecosystems.

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

Materials and methods

Stomach contents collection and analyses

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

To assess the prevalence of INS in alligator populations we applied Roughgarden's (1972, 1979) concept of total niche width (TNW; full range of food resources used by a population), which is subdivided into a between-individual component (BIC; variance in food resource use between individuals) and within-individual component (WIC; variance in food resource use within individuals), such that TNW = BIC + WIC. If BIC > WIC for a given population, then the diets of individuals are more diverse in comparison to each other than they are diverse within each individual. We divided BIC by TNW to generate an index of specialization that varied between 0 and 1, where 0 = pure generalist population (individuals completely overlap with population's resource use) and 1 = pure specialist population (individuals do not overlap at all with other individuals in the population). We chose to focus on the BIC/TNW index because it is simple to calculate and because other INS metrics generally produce similar results (Bolnick et al. 2002). Calculations of BIC/TNW are biased by the inclusion of individuals that only contain prey items from one prey group in their stomach (Bolnick et al. 2002), so we applied sorting rules to each dataset to limit bias in our INS results and produce more conservative BIC/TNW values (explanation in electronic supplemental materials).

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

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

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

Since diet variation can be caused by sexual and ontogenetic differences, as well as inherent temporal and spatial prey variability, we needed to control for these potentially confounding factors before we could quantify INS. Therefore, we tested each stomach contents dataset to see if the datasets varied as a function of the variables capture season, capture year, capture location, size, and sex (Table S1) using principal component analysis and multivariate analysis of variance (MANOVA; Araujo et al. 2007; explanation in electronic supplemental materials). If MANOVAs revealed that any of the independent variables were significant predictors of stomach contents variation in any given dataset, we divided the dataset into smaller subsets to remove the bias (e.g., splitting the dataset into male and female subsets to control for sex differences in diets). We chose the subsets of each dataset with sample sizes of at least 10 individuals for BIC/TNW analysis using the program IndSpec 1.0 (Bolnick et al. 2002), then converted the BIC/TNW values into E_{adj} values. We used the program's Monte Carlo procedure to test the null hypothesis that any observed variation in diet was caused by individuals sampling randomly from a shared resource pool (Araujo et al. 2007; explanation in electronic supplemental materials).

Stable isotope collection and analyses

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

Tissue-specific turnover rates can vary widely between species (Dalerum and Angerbjorn 2005). A diet-switch study of juvenile alligators (Rosenblatt and Heithaus 2013) revealed that the approximate complete turnover time of alligator plasma for $\delta^{13}C$ (252 days) was roughly half that of red blood cells (RBCs; 566 days). Therefore, if $\delta^{13}C$ values for an alligator were similar across these tissue types it would suggest that the mixture of carbon pools used across an eight month period prior to sample collection is similar to that used across a 19-month period prior to sample collection. Differing $\delta^{13}C$ values would indicate shifts in the relative contributions of different carbon pools across these timescales. For our analyses we used stable isotope data from plasma and RBC samples from 214 alligators collected between 2008 and 2012 from six sites (Table 1; see Rosenblatt and Heithaus (2013) for sample collection procedures and the electronic supplemental materials for laboratory analysis procedures).

Before assessing the prevalence of INS in the alligator populations using SIA we needed to remove the possibility that our results were affected by variable fractionation factors between the two tissues (Dalerum and Angerbjorn 2005). Therefore, we subtracted experimentally determined fractionation values (isotopic differences between tissues and diet) for each alligator tissue (+0.35‰ for plasma $\delta^{15}N$, -0.04‰ for plasma $\delta^{13}C$, +0.95‰ for RBC $\delta^{15}N$, and +0.03‰ for RBC $\delta^{13}C$; Rosenblatt and Heithaus 2013) from the δ values for each tissue. Then, MANOVAs were used to determine if the stable isotope datasets were significantly affected by the variables capture season, capture location, size, or sex. We only focused on the $\delta^{13}C$ values of the two tissues as the dependent variables because they contain information about nutrient origins. After controlling for possible confounding variables and the potential effects of fractionation factors, we determined correlation coefficients for each dataset to see if the relationships between the $\delta^{13}C$ values of plasma and RBCs were linear and positive (i.e., exhibited correlation coefficients close to one). We then employed linear regression to further examine the relationship between the $\delta^{13}C$ values of plasma and RBCs. If individual alligators exhibited stable foraging patterns over the long time periods represented by the two tissues, we would expect the $\delta^{13}C$ values of plasma and RBCs to be highly correlated, with linear regression best-fit lines characterized by high R^2 values and slopes close to one. Conversely, if alligators exhibited more variable foraging patterns we would expect best-fit lines characterized by low R^2 values and slopes farther away from one. All statistical analyses were performed in SPSS 17.0 (IBM, Armonk, NY, USA) and SigmaPlot 11.0 (Systat, Chicago, IL).

Results

Stomach contents

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

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

After subdividing each dataset to control for significant predictor variables, the resulting Shark River dataset was removed from further analyses because it was heavily skewed by two individuals that each consumed thousands of anchovies (Engraulidae). The remaining 28 populations and sub-populations only included 23 monophagous individuals between them and produced E_{adj} specialization values that varied widely, with a minimum of 0.03 and a maximum of 0.74 (mean = 0.39 ± 0.19 SD; Table 2). The Monte Carlo simulations revealed that despite the wide range of observed BIC/TNW values, all but one population exhibited significantly greater specialization than predicted by chance (Table 2). The E_{adj} values were not affected by sample size (linear regression: $R^2 = 0.007$, $P = 0.7$), but the E_{adj} values were significantly different between habitat types (t-test: $t_{26} = -2.7$, $P = 0.01$), with populations from lakes exhibiting lower values (mean = 0.35 ± 0.17 SD) than populations from coastal habitats (mean = 0.58 ± 0.14 SD).

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

Stable isotopes

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

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

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

Discussion

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

Consistent with our hypotheses, our findings suggest that one of the main drivers of INS, at least in the short-term, is habitat heterogeneity and prey community composition. Lower E_{adj} values in alligator populations inhabiting lakes could be a consequence of low habitat variation in lakes and their well-defined boundaries. For example, Lake Apopka in central Florida, whose alligator population was sampled several times across our datasets, has been a shallow, homogenous, turbid, algal-dominated lake lacking a diverse fishery since 1947 (Bachmann et al. 1999). In contrast, the estuarine habitats sampled across our datasets contain a diversity of aquatic habitats (freshwater, estuarine, marine) and have diffuse boundaries, thus potentially allowing for greater movement of alligators and greater ingress of possible prey taxa. In fact, movement studies indicate that alligators inhabiting lakes move shorter distances and occupy smaller ranges than alligators in coastal habitats, and lake alligators largely restrict themselves to littoral areas (Goodwin and Marion 1979; Rosenblatt et al. 2013). Together, these observations suggest that lake-bound alligators have access to less distinct habitat types and prey groups than coastal populations. Consistent with this hypothesis, our analyses indicated lake alligator populations used fewer prey categories present in their habitat when compared to non-lake populations, though this result was not statistically significant.

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

Our results further suggest that prey community composition can drive short-term INS because the E_{adj} values were negatively correlated with the number of mollusks consumed by a population as a percentage of the whole diet. We hypothesize that the presence of abundant easy-capture prey like mollusks in certain habitats may allow the majority of alligators in those habitats to take frequent advantage of a resource so easily found and consumed. However, when mollusks are not as abundant alligators must pursue more mobile prey that are harder to capture. These contrasting contexts would make each individual’s short-term diet in mollusk-rich habitats (i.e., lakes; Darby et al. 2006) more similar to conspecifics, thereby decreasing INS, but more different from conspecifics in habitats containing less abundant mollusks, thereby increasing INS (e.g., Baird et al. 1992; Tinker et al. 2008). In the latter context dietary variation between individuals could be caused by resource patchiness rather than behavioral specialization, but available evidence suggests that alligators do not move randomly through their environment because individuals visit the same foraging areas over multiple years (Rosenblatt and Heithaus 2011; Rosenblatt et al. 2013). Although individuals may return to similar locations for periods of time, their foraging trips take them to areas with prey supported by different carbon sources (e.g. marine versus freshwater production). Thus, INS in habitats dominated by more mobile prey could be caused by fine-scale associations between individual alligators and specific areas or by individuals learning to eat different prey.

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

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

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

SIA revealed that alligators generally exhibited highly consistent use of different carbon pools across longer time frames. The consistent δ^{13}C values we observed across tissues could have been caused by specialization on specific prey but could also be attributed to consistent use of specific habitats and movement patterns. We hypothesize that the latter explanation is more likely, i.e. that alligators specialize in certain behavioral patterns, like specific foraging and movement tactics. This possibility was partially accounted for in our study by separating analyses for individuals captured in different habitats, but because of their high mobility alligators captured in the same habitat still could move across the landscape in different ways. Our hypothesis is supported by a previous study of alligator movement patterns in the Shark River where alligators exhibited temporally stable variation in movement patterns (Rosenblatt and Heithaus 2011; Rosenblatt et al. 2013): half of the alligators regularly commuted between freshwater/estuarine and marine habitats and the stable isotope values of their skin indicated that they were consistently feeding in two different food webs, whereas other alligators limited their movements and feeding strictly to freshwater/estuarine habitats. Similar patterns appear to occur in sea turtles, although on a different time scale, in that individual turtles will use consistent “corridors” to move between nesting and foraging areas and will return to the same foraging areas repeatedly, or individuals from the same nesting populations may be either coastal or pelagic in their foraging habitats (see Heithaus 2013 for a review). Our study and others point to the difficulties in using SIA to infer INS behaviors as a standalone data source when turnover rates of even “fast” tissues are long, as in most reptiles (Rosenblatt and Heithaus 2013), because in such situations SIA fails to capture short-term dietary choices. Therefore, we echo previous studies in suggesting that INS studies should combine isotope data with other behavioral data where possible. We should also note that the turnover rate of alligator plasma is almost 50% of the turnover rate for alligator RBCs, thus inherently biasing our analyses towards strong correlations between the $\delta^{13}C$ values of the two tissues. However, despite this methodological artifact we are confident in our results because of the remarkable strength of the correlations across almost every alligator population we sampled.

Many current ecosystem management and conservation strategies assume that all apex predators in a population will have similar effects on prey populations. However, if behaviors vary consistently across individuals, as our study and those of other taxa (Bolnick et al. 2003) suggest, then one-size-fits-all conservation and management strategies may have unintended consequences in many systems. For example, the Shark River is part of the Everglades which is an ecosystem currently undergoing large-scale restoration (Doren et al. 2009). Restoration activities are expected to bring more freshwater to the area, thereby decreasing salinity and potentially increasing habitat quality for alligators that are dependent on freshwater (Mazzotti and Brandt 1994). Since many of the alligators in this system appear to specialize in exploiting the marine food web seasonally (Rosenblatt and Heithaus 2011), increased freshwater flow may positively impact this group by allowing them to access marine resources for a larger portion of each year (though the distribution of marine prey may change as well). However, individuals that do not currently take advantage of marine resources may not experience the same future benefits. In addition, the spatial scale of alligator movements, and therefore potential coupling of food webs and nutrient transport (Rosenblatt and Heithaus 2011), likely will change. As freshwater moves seaward, any individuals exploiting marine food webs will not need to move as far upstream for osmoregulation. Similarly, in northern Kenya, African wild dog (*Lycaon pictus*) populations outside of protected areas exhibit specialized feeding on smaller prey than populations inside protected areas (Woodroffe et al. 2007). Thus, if wild dog conservation efforts were solely aimed at bolstering large prey populations some wild dogs may see no benefit unless their feeding patterns are very plastic. Different restoration and conservation scenarios, therefore, may differentially benefit subsets of apex predator populations. As a result, restoration and conservation actions may not achieve their intended goals if individual behavioral specialization is not explicitly considered during the planning process.

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

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

Acknowledgements

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

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

Data source	Locations	Habitat type	Duration	Collection method	N
Stomach contents					
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
Stable isotopes					
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

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

Data source	Location	Sample date	Sex	Size (TL; cm)	N	BIC/TNW (E_{obs})	BIC/TNW MC (E_{null})	E_{max} (prey categories)	$E_{adjusted}$
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
Elsey 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

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

All others, $P = 0.3$

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

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

Figure captions

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

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

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