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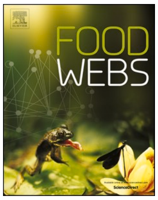

Seasonal frugivory drives both diet inconsistency and individual specialization in the generalist herbivore gopher tortoise

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ABSTRACT

Individual diet specialization, where individuals within a population exhibit distinct dietary patterns, can be influenced by shifts in ecological opportunity. One underexplored avenue of research is in investigating whether individuals switch foraging strategies (e.g., shifting from herbivory to frugivory) when ecological opportunity provides a pulse of limiting resources, such as fleshy fruits. This study investigates the influence of seasonal frugivory on diet consistency and specialization among generalist herbivores, specifically the gopher tortoise (*Gopherus polyphemus*), in southeastern Florida, USA. We hypothesized that increased frugivory during the wet season (June through November), coinciding with a resource pulse of fleshy fruits, leads to more inconsistent and specialized diets. Using radio telemetry to track individual tortoises and analyzing dissected fecal samples grouped into functional food categories, we applied Bayesian hierarchical modeling to examine diet consistency and specialization. Our results indicated that higher frugivory levels in the wet season correlate with greater diet inconsistency and specialization compared to the dry season. This pattern suggests that gopher tortoises may switch foraging strategies to exploit seasonal resource pulses of fleshy fruit, thus adopting more inconsistent and specialized diets. Additionally, important activities in the life history of the gopher tortoise, such as copulation, home range defense, and burrow construction, coincide with periods of increased fruit consumption and dietary inconsistency/specialization. Increased intake of carbohydrates and digestible energy from fleshy fruits may allow for more time in the tortoise's activity budget for these activities. Finally, by elucidating the relationship between seasonal frugivory and diet consistency/specialization, this research enhances our understanding of the mechanisms shaping ecological dynamics at the intraspecific level which can subsequently influence community-level interactions such as animal-mediated seed dispersal.

1. Introduction

Frugivory is a foraging strategy employed by diverse fauna which plays a critical role in maintaining biodiversity and ecosystem services (Jordano, 2000; Herrera, 2002; Bello et al., 2015). This foraging strategy involves the consumption of fruits and depending on the consumer, can vary in intensity and outcomes for seed dispersal (Marques Dracxler and Kissling, 2022; van Leeuwen et al., 2022). Beyond a simple foraging strategy, frugivory constitutes a crucial ecological interaction where animals meet their energetic and nutritional needs while plants receive dispersal services for their seeds (Jordano, 2000; Herrera, 2002; Jordano et al., 2011; Traveset et al., 2014). However, fruits are a spatiotemporally limited resource, available only in pulses dictated by flowering and fruiting phenology. Often, these resource pulses are aligned with seasonal environmental factors such as day-length, temperature, and precipitation (Mendoza et al., 2017; Cortés-Flores et al., 2019; Abrahms

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et al., 2021). Understanding how temporal patterns of frugivory influence ecological phenomena is crucial for advancing ecological theory and informing conservation strategies.

While some animals consume fruit year-round, others become more frugivorous by following seasonal resource pulses (Remis, 1997; Koike et al., 2008). In fact, the movement patterns of these seasonal frugivores may change to track the availability of fleshy fruit (Abrahms et al., 2021; Robira et al., 2023). While increasing their fruit consumption during periods of increased availability, seasonal frugivores may diverge from conspecifics in their resource use patterns (Fuh et al., 2022), which could be explained by interindividual diet variation (Araújo et al., 2011). Interindividual diet variation, also known as individual specialization, is when individuals diverge in their resource use patterns when compared to their population. Individual specialization can be caused by a variety of drivers that include competition, predation, and ecological opportunity (Bolnick et al., 2007; Araújo et al., 2011). Ecological opportunity can result from increased resource availability due to intra-annual resource pulses, such as those resulting from seasonal fruiting phenology (Bancroft et al., 2000; Redwine et al., 2007; Gerardo Herrera et al., 2008).

In some species, as resource diversity increases, so does the degree of diet specialization among individuals (Balme et al., 2020). Seasonal frugivory could lead to either lower or higher interindividual diet variation. For example, if all individuals switch to a highly profitable seasonally available resource (Schoener, 1986), diet variation should decrease. On the other hand, depending on the seasonally available resources and the tradeoffs involved in their consumption, the seasonal addition of fruits to an individual's diet might be accomplished by higher diet variation, which has received empirical support. In the case of the Egyptian fruit bat (*Rousettus aegyptiacus*), individual diets tend to exhibit greater specialization when there is an increase in fruit availability (Gerardo et al., 2008).

Gopher tortoises (*Gopherus polyphemus*) – widely recognized for their proclivity to create burrows that support over 350 commensal species (Diemer, 1986; Lips, 1991; Dziadzio and Smith, 2016; Melanson, 2021) – are primarily herbivorous (MacDonald and Mushinsky, 1988; Mushinsky et al., 2003). This species is a generalist consumer known to forage on upwards of 1000 plant species across its range (Ashton and Ashton, 2008), and although an efficient herbivore (Bjorndal, 1987), the gopher tortoise also engages in frugivory – acting as a prolific seed disperser (Carlson et al. 2003; Birkhead et al. 2005; Hanish 2018; Richardson and Stiling 2019; Figueroa et al. 2021). On occasion, this species will also scavenge, engage in coprophagy, and consume rocks and shells as gastroliths (Moore and Dornburg, 2014; Yuan et al., 2015). Due to its broad diet, this species is an ideal model for investigating individual variation in resource-use patterns, particularly in the floristically diverse pine rockland ecosystem of southeastern Florida (Trotta et al., 2018), a region where plant communities experience seasonal pulses of fleshy fruit production (Bancroft et al., 2000; Redwine et al., 2007).

In this study, we quantify patterns of individual diet consistency and specialization among conspecific gopher tortoises and investigate whether these patterns vary seasonally. We also explore whether variability in diet consistency and specialization is linked to seasonality and the consumption of fleshy fruits (i.e., frugivory). Given the wide niche breadth of our study species, the gopher tortoise (Ashton and Ashton, 2008), we hypothesize that there are marked differences in how specialized individual diets are. We further anticipate that in periods with greater fleshy fruit availability – such as the rainy season in south Florida (Lodge, 2017; Flora of North America Editorial Committee, eds. 1993+, 2023) – there will be greater diet specialization due to increased frugivory. Finally, we expect that as the amount of fruit consumption increases, so will the degree of diet specialization as has been found in previous studies on frugivory and diet specialization (Gerardo et al., 2008; Fuh et al., 2022).

2. Materials and methods

2.1. Site description

This study took place in Miami-Dade County, Florida, USA, in the globally imperiled pine rockland ecosystem (USFWS, 1999, Florida Natural Areas Inventory, 2010, World Wildlife Fund, 2014). Specifically, this work was conducted at an 830-ha complex of properties known as The Richmond Tract (Possley et al., 2020; Figueroa et al., 2023), in the rocklands surrounding Zoo Miami which serves as critical habitat for numerous endemic and federally listed species, as well as the population of gopher tortoises under study here (Possley et al., 2018; Whitfield et al., 2018, 2022; Figueroa et al., 2021). Southern Florida, where the pine rockland forests are located, has a subtropical climate where seasonal fluctuations in temperature are less pronounced than that of rainfall (Snyder et al., 1990; Lodge, 2017). Here, summer and fall are considered the wet season (June to November) and winter and spring the dry season (December to May) (Snyder et al., 1990; Lodge, 2017). As a result, the phenology of many plants in this community coincides with these seasonal changes in precipitation (Flora of North America Editorial Committee, eds. 1993+, 2023).

The pine rockland is the most floristically diverse ecosystem in southern Florida, containing over 430 plant species (Trotta et al., 2018), many of which are endemic to this region and ecosystem type. Its biotic community represents the confluence of temperate species at the southern extent of their geographic range and neotropical species at the northern extent of theirs. This ecosystem is fire-maintained and characterized by its scant, savanna-like canopy of endemic south Florida slash pine (*Pinus elliottii* var. *densa*), midstory of palms and shrubs, and understory of endemic, fire-dependent herbs such as Florida brickellbush (*Brickellia mosieri*), Carter's small-flowered flax (*Linum carteri carteri*), and deltoid spurge (*Euphorbia deltoidea* ssp. *deltoidea*) (Diamond and Heinen 2016; Possley et al. 2008). In addition to the diversity of plants they contain, pine rocklands provide habitat for a longtime inhabitant of this ecosystem that persists in remnant preserves to this day, the gopher tortoise (Simpson, 1920; Carr, 1940; Monroe, 1943; Enge et al., 2004; Whitfield et al., 2018, 2022; Figueroa et al., 2021).

2.2. Study species

The gopher tortoise is the only native tortoise found east of the Mississippi and Tombigbee rivers (Auffenberg and Franz, 1982), and has been documented as far southeast as Miami, Florida by early homesteaders (Simpson, 1920; Monroe, 1943), and at Cape Sable in the 1980s – which is at the southwestern tip of the Florida peninsula (Kushlan and Mazzotti, 1984; Waddle et al., 2006). The tortoises at our study site have been the subject of multiple studies regarding ecology and conservation (Whitfield et al., 2018, 2022; Figueroa et al., 2021), and are found in three disjunct spatial aggregations which we refer to as the East, South and West sites (Fig. 1). These aggregations of tortoises are due to a combination of the species' social behavior (Guyer et al., 2012), as well as the geology of this ecosystem which can limit the availability of deep sandy soils that facilitate burrowing (Hoffmeister et al., 1967; Whitfield et al., 2022). During the study, no tortoises migrated from one of these aggregations to another, so each site has a perfectly nested subset of individuals that occupy it.

Vegetatively, the plant communities in the West, South, and East sites are very similar where they fall within the pine rockland footprint. However, half of the burrows in the East aggregation were surrounded by invasive plant species such as Burma reed (*Neyraudia reynaudiana*), showy rattlebox (*Crotalaria spectabilis*), shrub verbena (*Lantana camara*), and bitter melon (*Momordica charantia*) just outside the pine rockland footprint (Fig. 1). Although there are contrasts in the plant communities inside and outside the pine rockland footprint, our estimates of individual diet specialization are calculated across the entire population of tortoises over the whole study period, thereby incorporating both spatial

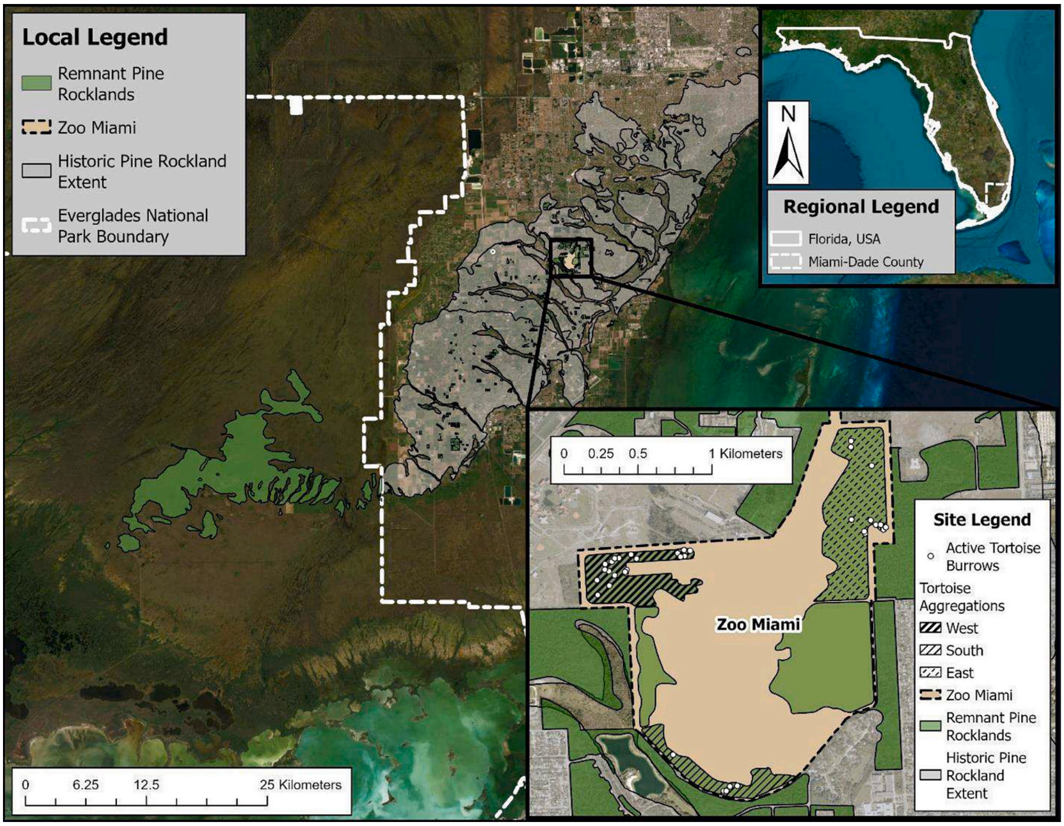

Fig. 1. Our study site, Zoo Miami, lies on the largest expanse of pine rockland habitat outside of Everglades National Park, known as The Richmond Tract in Miami-Dade County, Florida, USA.

and temporal differences in diet specialization into our population estimate.

2.3. Study design

2.3.1. Scat collection/dissection

This study was carried out over a 1.5-year period with scat collection beginning on May 11th, 2021, and ending on November 9th, 2022. We used radio telemetry to track wild gopher tortoises at The Richmond Tract twice weekly. If an individual tortoise defecated during handling, the fecal sample would be collected in a plastic bag and labeled with the tortoise's ID number, location, and date encountered.

Scats were dissected with forceps over laminated graph paper (29.59 cm × 21.01 cm), containing 5 mm × 5 mm grids as a static background reference to compare the relative contributions of food items to the total fecal volume. All food items recovered from the fecal sample were identified to the lowest taxonomic unit or qualified as their own category (e.g., fur/hair was recovered from multiple species and subsequently categorized jointly). After dissection, fecal contents were spread over the laminated graph paper and the relative contributions of each food item to the total scat volume was visually estimated; an approach widely used in dietary studies (Klare et al., 2011). One limitation of this method, however, is that it assumes the volume of different foods remains relatively consistent as fecal content. Considering the high digestive efficiency of the gopher tortoise for plant matter (Bjorndal, 1987), this may result in greater representation of animal remains than plant matter in feces, especially for fleshy fruits which have high water content and are more easily digested (Coombe, 1976).

Food item contributions were quantified as proportions of either 0.01, 0.05, or in increments of 0.05 all the way to the total scat volume of 1.00. If values <0.05 remained after quantifying the contributions of all food items, this amount was allocated to the most abundant food category from the sample. Of all the plant species consumed, only seeds and undigested pulp from endozoochorous (fleshy-fruited) species were considered as “fruit” in the sample (Ridley, 1930; Van der Pijl, 1982). While running oak (*Quercus pumila*) fruits (i.e., acorns) lack a fleshy mesocarp, we included them in the Fleshy Fruit category since acorns are usually sought after for consumption by turtles (Carlson et al., 2003; Elbers and Moll, 2011).

2.3.2. Aggregating food categories

Food items were ultimately aggregated into the following five functional food categories due to their distinct importance in gopher tortoise diets (Bjorndal, 1987; MacDonald and Mushinsky, 1988; Ashton and Ashton, 2008; Moore and Dornburg, 2014; Figueroa et al., 2021):

1. **Grasses** were all members of the plant family Poaceae.
2. **Legumes** were all members of the plant family Fabaceae.
3. **Other Plants** were an aggregation of all other plant material that did not qualify as Legumes or Grasses yet were part of the vegetative aspect of the tortoise diet.
4. **Fleshy Fruit** represents all endozoochorous fruits consumed by gopher tortoises, following dispersal syndromes from classical literature in seed dispersal ecology (Ridley, 1930; Van der Pijl, 1982).
5. Lastly, the **Animals** category captures all material that is of animal origin (e.g., snail shells, eggshells, bone, and mammal fur).

The motive for aggregating food items in this way rather than using the taxonomic classification of each food item was to reduce the dimensionality of the dataset while maintaining enough resolution to examine how different functional groups contribute to shifts in dietary composition as well as individual specialization (Newsome et al., 2015).

2.4. Statistical analysis

All statistical analyses were carried out in R version 3.3.0 (R Core Team, 2022).

2.4.1. Correspondence analysis to characterize spatiotemporal shifts in dietary composition

To quantify whether and how dietary composition varied between the wet and dry seasons, we performed a Correspondence Analysis in the easyCODA package (Greenacre, 2017, 2019). We decided on a Correspondence Analysis due to the compositional nature of our dataset, wherein each variable is proportionally scaled relative to the others, summing to a constant (usually one). This characteristic of compositional data presents unique challenges, as traditional statistical methods like PCA or NMDS, which assume independence and unboundedness among variables, might not effectively capture the inherent dependencies and ratios between components. CA, however, is specifically designed for handling such data. It treats the rows and columns of the contingency table as profiles, thus facilitating a more appropriate analysis of how dietary compositions are associated relative to each other. This multivariate analysis pinpoints which food categories contribute most to the composition of fecal samples across seasons, allowing us to gauge how food categories contribute to observed shifts in diet, and potentially individual consistency and specialization.

We performed the Correspondence Analysis to visualize how diets varied seasonally and then overlayed vectors that illustrate the magnitude of influence for each of the five food categories on the diet composition. Lastly, we drew 95% confidence ellipses for each level of season, ultimately resulting in a Discriminant Correspondence Analysis. We quantified the influence of each food category on the total dietary composition by calculating the inertia captured by each in the Correspondence Analysis.

After the Correspondence Analysis, we used the vegan package to perform Permutational Analyses of Variance (PERMANOVA) on the Bray-Curtis dissimilarity matrix of the original dataset (Oksanen et al., 2022). This allowed us to assess significant differences in the population diet composition between seasons.

2.4.2. Bayesian hierarchical modeling

To quantify temporal diet consistency and inter-individual diet specialization, we employed the Bayesian hierarchical modeling framework implemented by Coblentz et al. (2017) in the *rjags* package (Plummer et al., 2016). This approach models the proportions in each of the food categories within each sample and at higher hierarchical levels such as individuals and populations. Briefly, the proportions of each food category in the diet samples are modeled following a multinomial distribution which required scaling the proportions to lie between 0 and 100. The sample proportions are then assumed to follow a Dirichlet distribution at the next highest hierarchical level (here for example the individual from which the sample was taken) (see Coblentz et al., 2017 for modeling details).

3. Calculation

3.1. Quantifying individual consistency and specialization

To calculate temporal diet consistency and inter-individual diet specialization, we specified a Bayesian hierarchical model with samples nested within the individuals of origin. We then calculated the Proportional Similarity of samples (IC_{s_i}), which describes how similar the composition of a sample *s* is to the mean of all samples provided by individual *i*:

$$IC_{s_i} = 1 - 0.5\sum_j \left|p_{ij} - q_{ij}\right| \tag{1}$$

where p_{ij} is the contribution of food item *j* in a sample of individual *i*, while q_{ij} is the contribution of food item *j* in the overall diet of individual *i* (i.e., the mean of all individual *i*'s samples), as long as the individual provided more than one fecal sample in the dataset.

To quantify the amount of temporal diet consistency in the population, we first calculated the mean IC_{s_i} from all the samples belonging to individual *i* (N_{s_i}) [Eq. (2)]. We refer to this metric as Individual Consistency (IC_i).

$$IC_i = \frac{\sum_{s_i}\left(IC_{s_i}\right)}{N_{s_i}} \tag{2}$$

An IC_i closer to 0.00 indicates lower similarity between an individual's fecal samples and its overall dietary composition. On the other hand, an IC_i closer to 1.00 indicates that samples are closer to the overall dietary composition of individual *i*, hence a more consistent diet.

For inter-individual diet specialization, we calculated the sample-level proportional similarity to the population diet (IS_{s_i}), which quantifies how similar an individual's samples are to the population diet [Eq. (3)].

$$IS_{s_i} = 1 - 0.5\sum_j \left|p_{ij} - q_j\right| \tag{3}$$

where p_{ij} is the contribution of food item *j* in a sample of individual *i* and q_j is the contribution of food item *j* to the diet of the whole population. Like for IC_{s_i}, IS_{s_i} values were only calculated for individuals that provided more than one fecal sample.

Additionally, we estimated Individual Specialization (IS_i) like in IC_i [Eq. (4)], by calculating the mean of all IS_{s_i} values across the samples provided by each tortoise (N_{s_i}).

$$IS_i = \frac{\sum_{s_i}\left(IS_{s_i}\right)}{N_{s_i}} \tag{4}$$

An IS_i value closer to 0.00 indicates lower similarity between an individual's samples and the whole population whereas a value closer to 1.00 indicates higher similarity between individual's samples and the whole population.

To calculate the IC_i and IS_i values of all individuals, we ran the model on the full dataset and extracted the posterior draws for all individuals (14 individuals; 180 fecal samples total). We then plotted the posterior draws with the 95% Credible Intervals for each individual. This approach allowed us to robustly quantify the temporal consistency in diet of various individuals as well as their degree of individual resource use specialization (see Bolnick et al. 2002; Zaccarelli et al. 2013 and Coblentz et al. 2017 for more detail on the calculation of these metrics).

3.2. Quantifying temporal differences in diet consistency and specialization

After quantifying individual consistency and specialization for each tortoise in the population, we then ran the same model specification on two subsets of the full dataset: one containing only wet season samples and one containing only dry season samples. We subsequently extracted the IC_{s_i} and IS_{s_i} values for all samples in each season and plotted their posterior estimates together. This allowed us to examine seasonal differences in the sample-level measures of diet consistency and specialization, respectively.

To examine differences in IC_{s_i} and IS_{s_i} across seasons, we calculated the posterior distribution of the difference between wet and dry season estimates of both IC_{s_i} and IS_{s_i}. This allowed us to quantify the differences in sample-level diet consistency and specialization between seasons. For all estimates, we calculated the Bayesian probability of direction (PD) from the posterior distribution (Makowski et al., 2019). PD can be interpreted as the probability that the median of the estimate is strictly positive or negative, depending on which is most probable. This was done by dividing the number of posterior draws demonstrating the effect of interest (i.e., negative or positive values indicating the directionality of the effect), by the total number of posterior draws.

3.3. GLMM for influence of frugivory on diet specialization

Lastly, we used the Bayesian brms package (Bürkner, 2017) to construct a Generalized Linear Mixed Model (GLMM) which modeled posterior estimates of IC_{s_i} and IS_{s_i} as our response variables, to test if frugivory drives temporal diet inconsistency and inter-individual diet specialization, respectively. To incorporate uncertainty associated with the joint posterior distribution from the Bayesian analysis, we drew 30 samples from the posterior distribution for each sample and then used these draws as the response variable in the GLMM. We attempted to use the full posterior distribution for each sample but since the resulting data frame included over one million data points, it was impractical to execute the analysis with our computational power.

Given that IC_{s_i} and IS_{s_i} lie between 0.00 and 1.00, we specified a beta error distribution for both models with an uninformative prior. The estimates for IC_{s_i} and IS_{s_i} used as the response variable came from the two subsets of the full dataset used to calculate sample-level consistency and specialization in the wet and dry seasons. We specified the proportion of fecal volume comprised of fruit, the season in which samples were collected, and their interaction as our fixed effects. We then included a random effect to account for differences among individuals, inherently capturing spatial differences due to the nested nature of the tortoises across the three sites in addition to demographic-specific variation. Finally, we plotted the relationship between frugivory and individual consistency, as well as specialization, while stratifying by season to account for seasonal differences in the relationship.

4. Results

The Correspondence Analysis subsequently demonstrated that fruit consumption primarily explained the differences in dietary composition between the dry and wet seasons (Fig. 4), with fruit containing the highest inertia value of 0.54 compared to the other food categories which all fell below 0.35 (Table 1). PERMANOVA results confirmed that diets differed significantly in their composition in the wet season compared to the dry season ($F = 17.859$; $df_1 = 1$; $df_2 = 205$; $p < 0.0001$).

Individual tortoises varied greatly in their consistency (IC_i) and specialization (IS_i) with individuals who were more inconsistent in their foraging patterns also more specialized when compared to the population (Fig. 2). When plotting IC_{s_i} and IS_{s_i} values by season, a clear seasonal pattern in both diet consistency and specialization emerged (Fig. 3). In the wet season, diets were much more inconsistent and specialized than in the dry season, with a median difference in consistency of −0.11, and in specialization of −0.13, with neither of the credible intervals overlapping with 0.00. The PD estimate for the wet and dry season contrasts in both consistency and specialization was 100%. This indicated a high probability that diets in the wet season are both more inconsistent and specialized than in the dry season.

Table 1

Summary table for the Correspondence Analysis. Food categories are ordered from highest to lowest Inertia, which is the amount of variance captured by the food category. “Mass” refers to the total frequency of observations associated with a category while “ChiDist” measures the chi-squared dissimilarity between categories based on observed and expected frequencies, aiding in the calculation of distances in the low-dimensional representation of the data. “Dim. 1” and “Dim. 2” are the principal coordinate values for each category.

Seasonal Correspondence Analysis Results					
Food Category	Mass	ChiDist	Inertia	Dim. 1	Dim. 2
Fruit	0.101836	2.293578	0.535707	−2.939796	−0.40552
Animals	0.037826	2.954706	0.330233	0.18281	2.347988
Legumes	0.14599	1.498334	0.327749	0.010057	2.021206
Other Plants	0.067923	1.890907	0.24286	0.374998	−0.047709
Grasses	0.646425	0.491206	0.155972	0.410755	−0.524971

Modeling the relationship between fruit consumption and both sample-level diet consistency and specialization revealed a distinct negative relationship (Fig. 5). As diets became more frugivorous, they also exhibited greater inconsistency within an individual's fecal samples and higher specialization relative to the population (Table 2). Among the fixed effects and their interactions in both models, seasonality emerged as the predominant influence. The influence of seasonality was unequivocal in both models, with a PD value of 100%, verifying a seasonal effect. In the model for sample-level diet consistency, frugivory exhibited a PD value of 95.93%, indicating a high probability that increased frugivory leads to greater temporal diet inconsistency, regardless of seasonality. Similarly, in the diet specialization model, the PD value for frugivory was 92.83%. Though highly probably, the interaction between seasonality and frugivory was less pronounced in the sample-level diet consistency and diet specialization models, with PD values of 93.99% and 88.83%, respectively. These findings underscore the critical role of frugivory in driving dietary variability and specialization, even when accounting for individual and seasonal variations as controlled through our model's random effects.

5. Discussion

In the present study, we explored the temporal dimension of diet specialization (Novak and Tinker, 2015; Rosenblatt et al., 2015), by comparing how different individual diets were intra-annually, finding that in the two distinct south Florida seasons, wet and dry, there were marked differences in temporal diet consistency and inter-individual specialization. We documented substantial variation in the individual-level estimates of dietary consistency (IC_i) and specialization (IS_i), where individuals with less consistent diets also demonstrated more specialized diets when compared to the population. We then observed inter-seasonal differences in the sample-level measures of dietary consistency (IC_{s_i}) and specialization (IS_{s_i}), with less consistent and more specialized diets in the wet season than dry season, confirming that specialization is greater with increased precipitation as has been found in desert tortoises (*Gopherus agassizii*) (Murray and Wolf, 2013).

Dietary composition itself also varied inter-seasonally, with frugivory contributing most to this shift. Modeling sample-level diet consistency and specialization as a function of the interaction between season and frugivory – while accounting for individual-tortoise variation – revealed that frugivory is a major driver of both levels of diet specialization (i.e., temporal diet consistency and inter-individual diet specialization). As frugivory increased, irrespective of season, so did the variability of an individual's fecal samples when compared to its total diet, as well as how specialized the individual was when compared to the population.

As fruit availability increases intra-annually with precipitation in south Florida (Snyder et al., 1990; Lodge, 2017; Flora of North America Editorial Committee, eds. 1993+, 2023), gopher tortoises increasingly seek out this temporally limited resource which then facilitates diet specialization. Previous studies on another seasonal frugivore have found that the folivorous western lowland gorilla (*Gorilla gorilla gorilla*) becomes more frugivorous intra-annually by tracking the spatiotemporal availability of fleshy fruits (Remis, 1997; Robira et al., 2023). This seasonal tracking of fruits allows the gorillas to incorporate more digestible energy and a greater abundance of macronutrients into their diet (Masi et al., 2015). With the western lowland gorilla being a hindgut fermenter (Remis and Dierenfeld, 2004) – like the gopher tortoise (Bjorndal, 1987) – it is able to extract a great amount of energy from fibrous food items. Although adequate energy could be obtained without fruit, the digestive similarities between the gorilla and the gopher tortoise suggest that the readily available carbohydrates and digestible

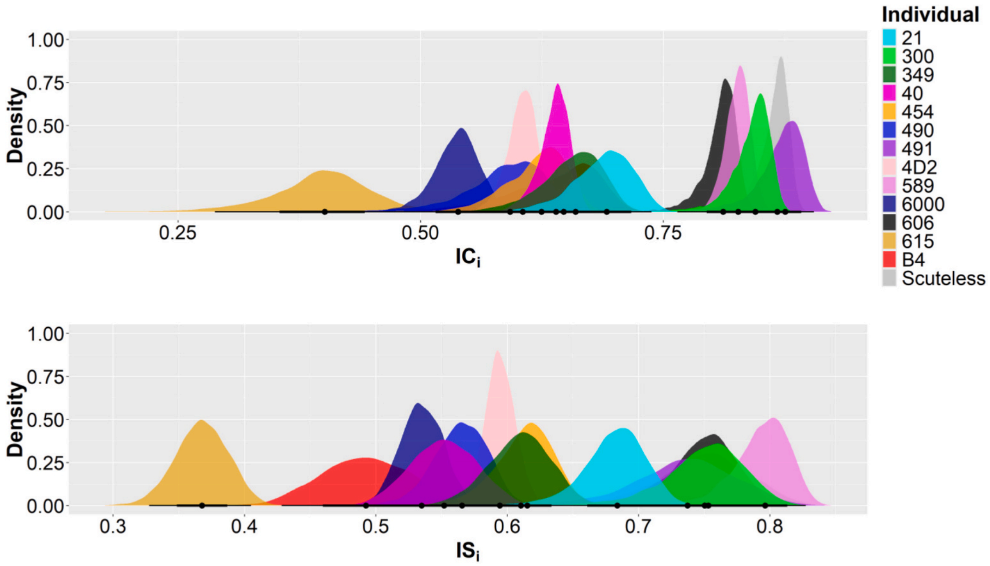

Fig. 2. Individual-level measures of diet consistency (IC_i; top panel) and specialization (IS_i; bottom panel) across all tortoises in the study that provided more than one fecal sample. Values closer to 0.00 indicate greater inconsistency/specialization whereas values closer to 1.00 indicate greater consistency and less specialization.

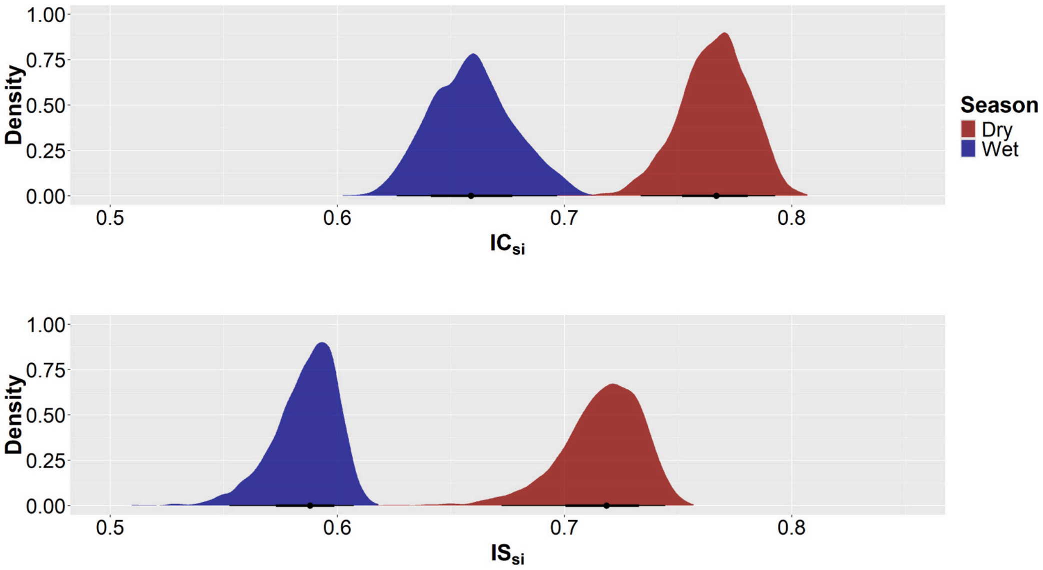

Fig. 3. Density plots illustrating seasonal shifts in sample-level measures of diet consistency (IC_{s_i}; top panel) and specialization (IS_{s_i}; bottom panel). Values closer to 0.00 indicate greater inconsistency/specialization whereas values closer to 1.00 indicate greater consistency and less specialization.

energy in fruit could allow for more time in the gopher tortoise's activity budget to copulate (Johnson et al., 2007), defend or expand home ranges (McRae et al., 1981; Masi et al., 2009), and burrow during periods of high fruit consumption (Eubanks et al., 2003). Interestingly, the timing of these documented behaviors in the gopher tortoise coincides with greater fruit consumption and specialization exhibited by the individuals of this study.

These results demonstrate that the gopher tortoise engages in opportunistic frugivory that facilitates diet specialization through a decrease in temporal diet consistency. This notion suggests that rather than falling in any one category between herbivory or frugivory (van Leeuwen et al., 2022), species – or individuals – may shift their diets to increase their consumption of temporally-limited resources such as fruit (Abrahms et al., 2021), thereby allowing them to specialize their diets. As demonstrated here, individuals in the population differentially engage in frugivory during the wet season. If all individuals engaged in the same degree of fruit consumption, there would be no individual specialization sensu Bolnick et al. (2003), but rather a uniform seasonal shift in diet where all individuals would exhibit the same feeding habits.

A likely explanation is that peaks in gopher tortoise activity patterns coincides with the wet season in the south Florida (Douglass and Layne, 1978; Lodge, 2017). In this time, female tortoises are usually gravid with eggs and juvenile tortoises experience increased growth rates (Rostal et al., 2014). Between age classes as well as between males and females, there are different energetic and nutritional requirements which are met by the increased consumption of legumes by growing juveniles and animal material by gravid females (Wilson et al., 1994; Moore and Dornburg, 2014). These differences in energetic and nutritional requirements among individuals at the intra-annual scale may explain the marked differences between individuals and their dietary habits. The ramifications of these findings are that individuals may engage in different degrees of frugivory and differentially participate seed dispersal as they become increasingly specialized, suggesting that conspecifics can provide unique seed dispersal services through diet

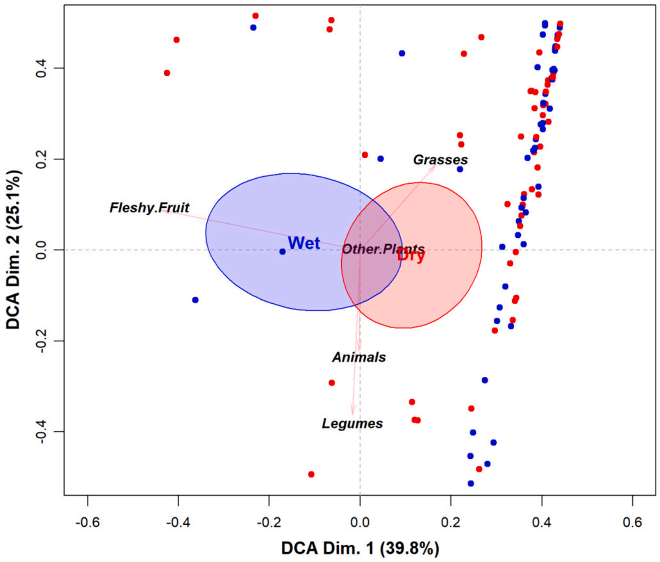

Fig. 4. Discriminant Correspondence Analysis (DCA) depicting seasonal shifts dietary composition, with 95% confidence ellipses around each season. Wet season is blue and Dry season is red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

specialization rather than through morphological or behavioral differences alone (Zwolak, 2018; Zwolak and Sih, 2020), although they may be related.

By unraveling the temporal differences in individual diet specialization that is driven by frugivory, this research contributes to our understanding of the mechanisms shaping ecological dynamics at the intraspecific level that can subsequently influence community-level interactions such as frugivory and seed dispersal (Zwolak, 2018; Marques Dracxler and Kissling, 2022; van Leeuwen et al., 2022). Such insights have implications for conservation and management efforts, as they can identify vulnerable populations lacking the appropriate resource diversity for their maintenance and can inform the ways in which habitat management can facilitate their persistence. Moreover, a comprehensive understanding of individual specialization provides a foundation for predicting responses to environmental perturbations and enhances our ability to conserve biodiversity in the face of global change. We encourage future studies that quantify how the consumption of resources that facilitate diet specialization, such as frugivory, varies temporally and what the subsequent implications are for the seed dispersal services provided.

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Ethical approval

All applicable institutional and/or national guidelines for the care and use of animals were followed.

Consent to participate

Not applicable.

Consent for publication

Not applicable.

Availability of data and material

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Code availability

The code written and used during the current study are available from the corresponding author on reasonable request.

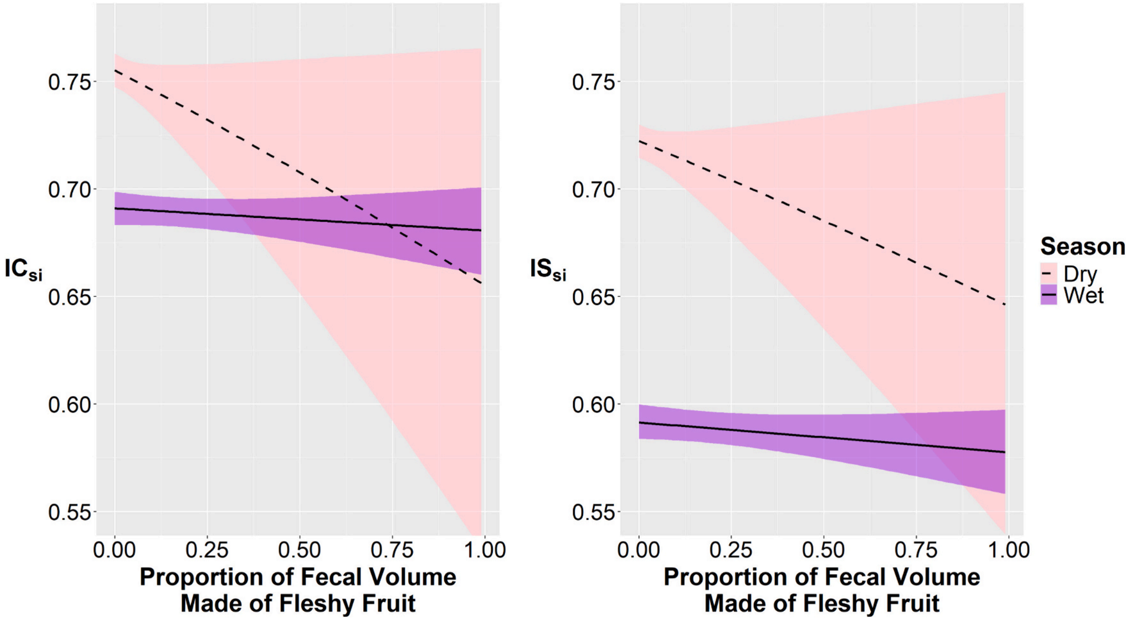

Fig. 5. Regression plots from the Generalized Linear Mixed Models, illustrating the influence of frugivory on sample-level diet consistency (IC_{s_i}; left panel) and specialization (IS_{s_i}; right panel). Values closer to 0.00 indicate greater inconsistency/specialization whereas values closer to 1.00 indicate greater consistency and less specialization.

Table 2
Summary table for the effect of frugivory and seasonal differences on the sample-level measures of diet consistency (IC_{s_i}) and specialization (IS_{s_i}). Posterior median estimates, error estimates, lower 95%, and upper 95% credible intervals (CI) are displayed in log-odds, along with the probability of direction (PD), and model convergence diagnostics (e.g., Rhat, Bulk Effective Sample Size (ESS), and Tail ESS) for the estimates.

Summary Table for Effect of Frugivory and Seasonality on IC_{si} and IS_{si}

Metric	Variable	Est.Error	Lower 95% CI	Median Estimate	Upper 95% CI	PD	Rhat	Bulk_ESS	Tail_ESS
IC_{si}	Intercept	0.022	1.084	1.126	1.168	100.00%	1.000	19,192.72	12,372.95
IC_{si}	Frugivory	0.271	−1.014	−0.482	0.065	95.93%	1.000	10,863.70	10,404.71
IC_{si}	Season	0.027	−0.374	−0.321	−0.270	100.00%	1.000	24,291.26	12,342.25
IC_{si}	Frugivory:Season	0.276	−0.125	0.433	0.970	93.99%	1.000	10,548.59	11,333.72
IS_{si}	Intercept	0.020	0.917	0.955	0.994	100.00%	1.000	16,202.34	11,918.04
IS_{si}	Frugivory	0.237	−0.809	−0.354	0.121	92.83%	1.000	12,880.79	11,964.24
IS_{si}	Season	0.023	−0.630	−0.585	−0.541	100.00%	1.000	26,825.45	12,373.41
IS_{si}	Frugivory:Season	0.241	−0.184	0.297	0.759	88.83%	1.000	12,895.80	12,406.16

Declaration of authorship

AF conceptualized the project, carried out the fieldwork, performed the data analysis, and wrote the manuscript. KC provided guidance in the data analysis phase and provided comments and suggestions in the writing of the manuscript. AH assisted AF in much of the scat collection and dissection which was crucial to the completion of the project. LC provided expert help in plant identification for the scat analysis. JV continued scat collection for about one-third of the study period which was crucial to increasing sample size. HL guided the execution of the study and provided multiple rounds of comments and revisions. MSA worked closely with AF in the framing and execution of the writing and data analysis. SMW provided the infrastructure to conduct this work, joined in the fieldwork, and helped with writing.

Declaration of Generative AI in Scientific Writing

We, the authors, have no declarations of interest to report.

CRediT authorship contribution statement

Adrian Figueroa: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation. **Kyle Coblentz:** Writing – review & editing, Visualization, Validation, Supervision, Methodology, Formal analysis. **Alyssa Herrera:** Methodology, Investigation, Data curation. **Lydia Cuni:** Methodology, Investigation, Data curation. **Jennifer Villate:** Methodology, Investigation, Data curation. **Hong Liu:** Writing – review & editing, Validation, Supervision, Project administration. **Marcio Silva Araujo:** Writing – review & editing, Visualization, Validation, Supervision, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Steven M. Whitfield:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Project administration, Investigation, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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