



Nested diets: a novel pattern of individual-level resource use

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Many generalist populations may actually be composed of relatively specialist individuals. This ‘individual specialization’ may have important ecological and evolutionary implications. Although this phenomenon has been documented in more than one hundred taxa, it is still unclear how individuals within a population actually partition resources. Here we applied several methods based on network theory to investigate the intrapopulation patterns of resource use in the gracile mouse opossum *Gracilinanus microtarsus*. We found evidence of significant individual specialization in this species and that the diets of specialists are nested within the diets of generalists. This novel pattern is consistent with a recently proposed model of optimal foraging and implies strong asymmetry in the interactions among individuals of a population.

Generalist populations using a wide range of resources may actually be composed of individual specialists (West 1986, 1988, Werner and Sherry 1987, Svanbäck and Bolnick 2007). For example, the finch *Pinaroloxias inornata* in Cocos island uses a diversity of resources, including seeds, nectar and insects, but each individual consistently specializes on a single feeding strategy (Werner and Sherry 1987). This ‘individual specialization’ (Bolnick et al. 2003) in turn may have important ecological and evolutionary consequences, imparting more stable population dynamics (Lomnicki 1988, Kendall and Fox 2002, 2003) and potentially generating frequency-dependent disruptive selection (Bolnick 2004, Bolnick and Lau 2008).

Although individual specialization has been already documented in more than 100 vertebrate and invertebrate taxa (Bolnick et al. 2003), it is still unclear how exactly individuals within a population partition resources. For example, a population may be composed of generalists only, specialists only, or a combination of both (Fig. 1). If there are specialist and generalist individuals in the population, but the diets of the specialists are ordered subsets of the generalists’ diets (Fig. 1b, Svanbäck and Bolnick 2005), we would expect diets to be nested (Atmar and Patterson 1993). Alternatively, individual diets may be overdispersed (Fig. 1c), corresponding to continuous diet variation (Price 1987, Robinson et al. 1993, 1996, Robinson 2000, Bolnick 2004, Eklöv and Svanbäck 2006) or individuals may form groups specialized on different resources (Fig. 1d), which would constitute discrete diet variation (Smith 1990, 1993, Pfennig 1992). If diet variation is tightly linked to morphology, its

description is straightforward and can be done based on morphological variation. For example, tadpoles of the spadefoot toad *Scaphiopus multiplicatus* have a carnivore and an omnivore morph, which differ strikingly in morphology and diet (Pfennig 1992). However, often times the basis of resource variation is not morphological, but rather related to behavioral or life-history traits (Bolnick et al. 2003). For example, in the Cocos finch individuals exploiting different resources are morphologically similar and diet variation is caused by learning constraints (Werner and Sherry 1987). In those cases, the description of resource variation in terms of phenotypes will not be trivial.

The description of the patterns of diet variation in natural populations can be greatly improved if we use approaches that are based on diet per se and do not depend on the a priori identification of phenotypes. For example, a novel recent approach based on network theory revealed an unprecedented pattern of discrete diet variation in which individuals form clusters specialized on different resources (Araújo et al. 2008). How frequent this and other potential patterns of diet variation (Fig. 1) are in natural populations is still an open question. In the present paper we applied different approaches based on network theory (Bascompte et al. 2003, Araújo et al. 2008) to investigate the patterns of resource use in the gracile mouse opossum *Gracilinanus microtarsus*. This species shows individual specialization (Martins et al. 2008) and shows high recapture rates in the field, allowing for longitudinal sampling. By revealing the actual patterns of resource use at the individual level, we provided a better description of the phenomenon of individual specialization that gives new insights on its underlying mechanisms.

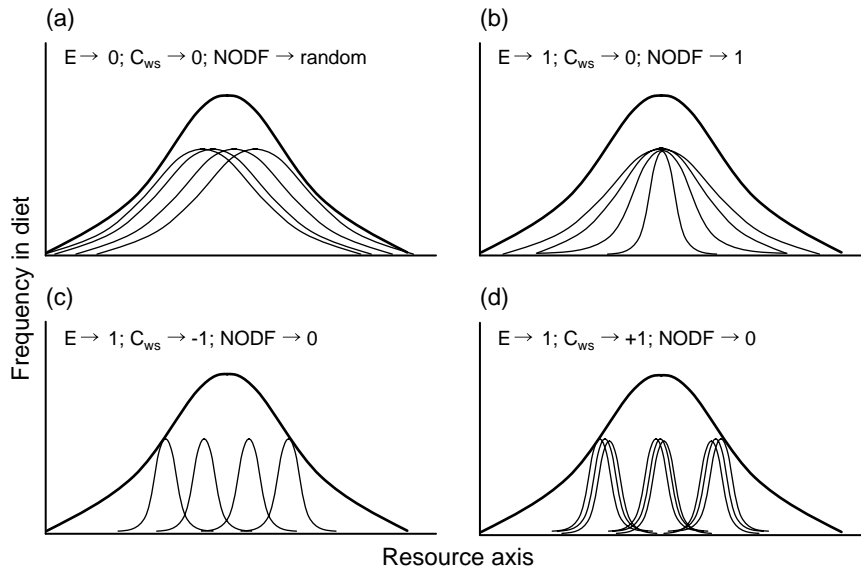


Figure 1. An illustration of four alternative ways in which individuals can subdivide the population niche (thick curve) and the expected behaviour of the E measure of interindividual diet variation, the C_{ws} clustering coefficient, and the NODF measure of nestedness. E varies from 0 to 1 and higher values indicate higher diet variation. C_{ws} varies from -1 to $+1$: low negative values indicate diet overdispersion and positive high values indicate diet clustering. NODF varies from 0 (no nestedness) to 100 (perfect nestedness). (a) individual niches (thin curves) overlap greatly with the population niche; (b) there are both specialist and generalist individuals in the population, and the diets of specialists are nested within the diets of generalists; (c) individuals overlap little with the population and with each other; (d) individuals form clusters that use specific subsets of the population niche. Unlike the idealized diagrams shown here, real populations are likely to contain a mixture of these four situations.

Methods

Study species

The gracile mouse opossum *Gracilinanus microtarsus* is a solitary, arboreal, nocturnal, short-lived (1–2 years) didelphid marsupial that inhabits the Atlantic rainforest and forested areas of the cerrado (savanna-like vegetation) in southeastern and southern Brazil (Emmons and Feer 1997, Gargaglioni et al. 1998). This species feeds on a wide range of resources, such as insects, arachnids, isopods, snails and fruits (Martins and Bonato 2004, Martins et al. 2006), and its diet composition has been shown to be strongly affected by sex and season in the cerrado (Martins et al. 2006). Additionally, individual-level diet variation has been demonstrated in one population of the species inhabiting an area of cerrado in southeastern Brazil (Martins et al. 2008).

Study site

Our study was carried out at the Reserva Biológica de Mogi Guaçu (RBMG) ($22^{\circ}15'22''S$, $47^{\circ}08'47''W$), located in the city of Mogi Guaçu, southeastern Brazil. Vegetation at the RBMG consists of cerrado, which is a tropical savanna formation comprising different vegetation physiognomies that differ in the density and composition of plants of the woody layer and the ground layer, forming a continuum from open and dry grassland to dense forest (Goodland 1971, Oliveira-Filho and Ratter 2002, Silva and Bates 2002). The RBMG is a remnant of the physiognomy locally known as ‘cerrado sensu stricto’, which is woodland

with scattered trees 5–8 m tall and closed scrub. Mean annual temperature and rainfall in the study area are $21^{\circ}C$ and 1430 mm, respectively. The climate of the region has two well-defined seasons: a warm-wet season from October to March (hereafter ‘wet season’) and a cool-dry season from April to September (‘dry season’). The abundance of arthropods and fruits changes markedly with seasons, being much higher in the wet season (Pinheiro et al. 2002, V. Bonato unpubl.). Moreover, different insect orders peak at different seasons, plants of the woody layer fruit at the end of the dry season, and those of the ground layer fruit at the end of the wet season/beginning of the dry season.

Data collection

The diet of *G. microtarsus* was determined by the analysis of faeces. The use of faeces to determine the diet of a species has the unquestionable advantage that animals need not to be killed (Dickman and Huang 1988). The main limitations of this approach to diet determination are potentially two-fold: differential digestibility of dietary items (Hume 2006) and individual variation in digestibility of different prey items (Munn and Dawson 2006). The faeces-analysis approach has been very effective to determine the diet of several species of small Neotropical marsupials (Martins and Bonato 2004, Martins et al. 2006, Leiner and Silva 2007, Martins et al. 2008). These studies have successfully recovered not only hard- and soft-bodied invertebrate prey items from faeces but also flower and fruit parts, suggesting that differential digestibility of food items does not seem to hamper the inference of dietary diversity in small Neotropical marsupials. Information on individual

variation in digestibility of different prey on the other hand is not available for small Neotropical marsupials.

Individuals of *G. microtarsus* were captured from November 2005 to March 2006 (wet season) and from May to August 2006 (dry season). Sampling was done every month, over 10 consecutive nights each month. Individuals were trapped and marked with a numbered ear tag and their sex and age were recorded. Age was recorded based primarily on the sequence of tooth eruption (Macedo et al. 2006). We set an 11×11 trapping grid with 121 trapping-stations located 15 m from each other. A Sherman live-trap (dimensions $7.5 \times 9.0 \times 23.5$ cm) was set on trees at each trapping-station about 1.75 m above ground and baited with banana and peanut butter. Faeces on the trap floor and those defecated by individuals during manipulation were collected and preserved in 70% ethanol. Faeces were transported to the laboratory and analysed with a stereoscope. The food resources were identified to the level of order and, in some cases, to family and genus using taxonomic keys (Borror and DeLong 1988) and/or by direct comparison with a reference collection of arthropods and fruits collected in the study area. We acknowledge that lumping different prey into broad categories such as order and family might potentially underestimate diet variation. For example, let's say that one individual marsupial specializes on a single family of beetles and another individual specializes on a different family. By lumping these two categories into Coleoptera, these two individuals will have the same diet, decreasing the estimate of diet variation for the population. However, if we still find diet variation even after such lumping procedure we can assume that there is diet variation, and that we actually have conservative estimates of the degree of diet variation in the population. The contribution of each food resource to the diet of individual *G. microtarsus* was determined by counting the number of individual prey or fruits present in faeces. We counted prey items in a way that we obtained conservative estimates of the number of items in faeces. Because of fragmentation of prey items, sometimes we had to infer the number of items based on parts of a prey's body (e.g. legs, mandibles). If for example we found two ant legs, there was no way of knowing if both legs came from a single ant or from two ants. In those cases, we took a conservative approach and counted these two legs as one single item.

Data analyses

It has been demonstrated that sex and season are important factors in not only determining the diet of *G. microtarsus* (Martins et al. 2006) but also the degree of among-individual diet variation (Martins et al. 2008). For that reason, we analyzed samples from different seasons and sexes separately.

Interindividual diet variation

In order to measure the degree of interindividual diet variation we used the index E , based on a network approach. This index is analogous to previously proposed indices of diet variation, but differs in that it has known statistical properties and is based on the pairwise diet overlap between individuals instead on the overlap between

individuals and the population. For details on the index, readers are referred to Araújo et al. (2008) and to the Online Supplement 1. Basically, E ranges from 0 when individual diets are identical and there is no diet variation, towards 1 as diet variation increases (Fig. 1). We note that this is an important difference between E and previous measures of diet variation, in which lower values indicate higher diet variation (Bolnick et al. 2002). Additionally, since individuals were recaptured over different time scales, ranging from days to months, we had the opportunity to test if degree of individual specialization depends on the time scale over which individuals are sampled. We did so by testing the correlation between the PS_i index of individual specialization, which measures the overlap between an individual i 's diet and the population diet (Bolnick et al. 2002), and the number of consecutive months over which an individual was recaptured. PS_i varies from 0 to 1, with lower values indicating higher specialization, so that a positive relationship between the time span of individual recaptures and PS_i would indicate that specialization is greater over shorter time scales and vice-versa.

Diet variation may arise by individuals sampling randomly a shared distribution of resources if information on individuals' diets is limited (e.g. few diet items in feces). We, therefore, tested the empirical values of E against a null distribution of E -values. We used a bootstrap procedure in which each individual was reassigned the same number of prey items that it was observed eating, drawn randomly from the population diet distribution via multinomial sampling (Araújo et al. 2008). Calculating E for each resampled population (we used 10 000 iterations), the null hypothesis can be rejected if the observed $E > 95\%$ of the null values. We used the program DIETA1.0 to calculate E and to perform simulations (Araújo et al. 2008). The PS_i indices were calculated in IndSpec1.0, a program to calculate indices of individual specialization (Bolnick et al. 2002). Additionally, we double checked our results with a rarefaction approach to assess the reliability of our sample sizes by testing the effects of reduced sampling effort on E . We randomly reduced the number of prey items recorded for individuals in the population until a given fraction of the total sampling effort. We generated rarefied samples of 95%, 85%, 75%, ..., 25% of total sampling effort and calculated E -values for each rarefied sample (we used 1000 replicates for each fraction).

Clustering

For a given level of diet variation (E), individuals may vary continuously along the niche axis (Fig. 1c) or form diet clusters (Fig. 1d). These different patterns of organization, in turn, can be captured with the recently proposed index C_{ws} , which varies from -1 to $+1$ (Araújo et al. 2008). C_{ws} will be positive and tend towards $+1$ when diet variation is clustered and it will be negative and will tend to -1 when diet variation is continuous. Combined with E , this index can be a useful tool in identifying the patterns of resource use within populations. For example, if there is no diet variation both E and $C_{ws} \rightarrow 0$ (Fig. 1a). If diet variation is continuous, so that individual niches overlap little with each other, $E \rightarrow 1$ and $C_{ws} \rightarrow -1$ (diets are overdispersed; Fig. 1c). If diet variation is discrete, so that individuals form

discrete dietary groups, $E \rightarrow 1$ and $C_{ws} \rightarrow +1$ (diets are clustered; Fig. 1d). Finally, if there are specialist and generalist individuals in the population, but the diets of the specialists are ordered, predictable subsets of the generalists' diets, $E \rightarrow 1$, but $C_{ws} \rightarrow 0$ (Fig. 1b), because although there is diet variation individuals neither form distinct clusters nor have overdispersed diets. Details on this index can be found in Araújo et al. (2008) and in the Online Supplement 1.

The significance of positive and negative values of C_{ws} can be tested with a null model approach similar to that described for E . Calculating C_{ws} for each resampled population (we used 10 000 iterations), there is evidence of clustering if $C_{ws} > 0$ and higher than 97.5% of the null C_{ws} values, or evidence of overdispersion if $C_{ws} < 0$ and lower than 97.5% of the null C_{ws} values. We used DIETA1.0 to calculate C_{ws} and to generate null distributions (Araújo et al. 2008). We also performed a rarefaction analysis similar to that described for E to test the effect of sampling effort on C_{ws} .

Nestedness

Resource use by individuals within a population can be described by a matrix \mathbf{R} , in which rows represent individuals, columns depicts resources types and the elements $r_{ij} = 1$ if the individual i used the resource j and zero otherwise. Therefore, \mathbf{R} qualitatively describes the use of different resource types by individuals and can be used to investigate nestedness. There are several distinct metrics to measure nestedness (Atmar and Patterson 1993, Almeida-Neto et al. 2008). In this study, we used the recently developed NODF measure of nestedness, which has conceptual advantages when compared with other metrics (Almeida-Neto et al. 2008). NODF will tend to 100 for highly nested matrices and tend to zero when individuals show other nonrandom patterns of resource use, such as overdispersed (Fig. 1c) and clustered diets (Fig. 1d). Random matrices will show intermediate NODF values depending on its size and the number of individual-resource interactions recorded (Fig. 1a).

As in the case of E and C_{ws} , nestedness may arise by individuals sampling randomly a shared distribution of resources. Thus, we tested the empirical values of NODF against a null distribution of NODF-values. We generated theoretical populations in which the probability that an individual i feeds on a resource j is:

$$p(ij) = \frac{1}{2} \left(\frac{k_i}{B} + \frac{k_j}{A} \right) \quad (1)$$

in which k_i is the number of resource types consumed by individual i and k_j is the number of individuals that consume resource type j , B is the number of resources and A is the number of individuals sampled (Bascompte et al. 2003). Calculating NODF for each resampled population (we used 10 000 iterations), the null hypothesis can be rejected if the observed NODF for individuals $> 95\%$ of the null values. We used the program ANINHADO to calculate NODF for individuals and to perform simulations (Guimarães and Guimarães 2006).

Nestedness may also be affected by reduced sampling effort, because the diets of individuals with limited

information might appear as subsets of the diets of the more thoroughly sampled individuals, causing nestedness. We therefore performed a rarefaction analysis similar to that done for E and C_{ws} . All rarefaction analyses were performed in MATLAB 7.4 and the script is available from authors upon request.

Results

In the following, we present the results on adult individuals only, since juveniles were very rarely captured. The average (range in parentheses) number of recaptures per individual was 7.7 (2–36) and recapture rates were higher in the dry season in both sexes (Table 1), although differences were not significant (males: Mann–Whitney $U = 145.0$, $p = 0.146$; females: $U = 110.0$, $p = 0.146$). The average (range) number of prey items per individual was 67.8 (4–500). In the dry season, *G. microtarsus* relied almost entirely on Isoptera (termites), consuming other resources in very low proportions (Fig. 2). In the wet season, the population niche expanded via a shift to a diet dominated by the fleshy fruit *Miconia* sp. and Coleoptera (Fig. 2). Isoptera, Hymenoptera (ants), and Lepidoptera (larvae) were still consumed in the wet season, but in lower proportions (Fig. 2).

We found low but significant diet variation within both sexes in both seasons (Table 1). The degree of diet variation was similar between males and females and there was a trend of slight higher diet variation (higher E values) in the wet season (Table 1), which may have been caused partly by the lower recapture rates in this season. However, the rarefaction analyses showed that the observed E -values were not a result of sampling biases (Fig. S1; Online Supplement 2). We found no correlations between the number of months over which individuals were recaptured and the PS_i index of individual specialization (all p -values > 0.45) except for females in the wet season, in which shorter time scales were associated with lower PS_i values (Pearson's $r = +0.507$; $p = 0.013$) and therefore higher individual specialization (recall that lower PS_i values correspond to higher individual specialization). We did not find any evidence of clustering or overdispersion (Table 1) and no effects of sampling effort on C_{ws} (Fig. S2; Online Supplement 2). Additionally, we found high, significant nestedness in both sexes in the wet season and in males in the dry season (Fig. 3). Rarefaction analyses indicated that nestedness was not the result of sampling biases in our data (Fig. S3; Online Supplement 2).

Discussion

Our results indicate the presence of individual specialization in the studied population of *G. microtarsus*, further corroborating previous findings for another population (Martins et al. 2008) and suggesting that this is a common phenomenon in this species. Moreover, we describe an unprecedented pattern of individual-level diet variation, in which the population is composed of generalist and specialist individuals and the diets of specialist individuals are ordered, predictable subsets of the diets of the generalists.

Table 1. The E and the C_{ws} measures of interindividual diet variation and clustering in the gracile mouse opossum *Gracilinanus microtarsus*. Diet variation and clustering were measured in males and females in the dry and wet seasons. 'Average (re)captures' represent the average number of captures and recaptures per individual. p-values were obtained in Monte Carlo bootstraps (10 000 simulations). E varies from 0 to 1 and higher values indicate higher diet variation; C_{ws} varies from -1 to $+1$, where negative values indicate overdispersion and positive values indicate clustering of diets.

Sex	Dry season				Wet season			
	E	C_{ws}	n	Average (re)captures	E	C_{ws}	n	Average (re)captures
Males	0.2780***	-0.0006^{NS}	10	9.9	0.3396*	$+0.0031^{NS}$	22	5.1
Females	0.2735***	$+0.0137^{NS}$	7	14.3	0.3523**	-0.0069^{NS}	23	7.1

NS: non-significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. n: number of individuals sampled

In the following paragraphs we elaborate on possible underlying mechanisms for this novel pattern as well as its ecological implications.

Gracilinanus microtarsus had a relatively narrow diet breadth in the dry season, feeding mainly on Isoptera (termites), but used a broader range of resources in the wet season, when it switched to a diet dominated by the seasonally abundant fruit *Miconia* sp. and Coleoptera. Population niche expansion in the wet season has been also documented for four species of frogs in another area of the *Cerrado* biome (Bolnick et al. 2007, Araújo et al. 2009) suggesting that this might be a general pattern in *Cerrado* communities. Resource abundance peaks in the wet season in the *Cerrado* (Pinheiro et al. 2002, V. Bonato unpubl.) and the observed niche expansion may be suggestive of a seasonal interspecific competitive release if interspecific competition is strong in the dry season, when resources

are scarce, but weak in the wet season, when prey are abundant. Future studies should investigate not only the generality of this pattern of seasonal niche variation in tropical savannas, but also try to quantify competitive interactions in these communities.

An important task when studying interindividual diet variation is to identify its potential underlying mechanisms. At a first level, diet variation among individuals may arise simply due to fine scale differences in the spatial distribution of resources if individuals forage in different places (Durell 2000). As a consequence, we cannot rule out the possibility that the observed diet variation results at least partly from the patchiness of resources in the area. Moreover, diet differences may be exaggerated by direct interference between individuals, in which dominant individuals secure preferred resources and force subordinate individuals to feed on suboptimal resources (Goss-Custard and Durell 1988). Dominance hierarchies have already been documented in other marsupials (Croft and Eisenberg 2006, Mclean et al. 2009) and might as well be present in *G. microtarsus*. We lack, however, information on the spatial distribution of resources as well as behavior and social organization (if any) in *G. microtarsus* to determine the importance of these factors in generating diet variation.

The above mentioned mechanisms provide plausible explanations for the presence of diet variation per se, but would very unlikely explain the presence of nestedness. For example, one could imagine the spatial distribution of resources to be nested within each other. If opossums' home ranges are also nested and match exactly the nested distribution of resources, we would expect diets to be nested as a mere consequence of the spatial distribution of resources and individuals. The available data indicate that *G. microtarsus* home ranges are on average 1300 m^2 and do overlap, but there is no evidence that they are nested (Fernandes 2007). Therefore, although the interaction between the spatial distributions of resources and home ranges may in part explain diet variation in *G. microtarsus*, other mechanisms must cause nestedness.

Diet variation may result from intrinsic phenotypic differences between individuals (e.g. behavioural, physiological) that generate different individual diet preferences (Bolnick et al. 2003). Recently, Svanbäck and Bolnick (2005) proposed a theoretical framework that provides a mechanistic explanation for individual specialization based on optimal foraging theory that is consistent with the nested pattern that we documented. According to their 'shared preferences' model, individuals have identical rank preferences for different resources, but differ in their

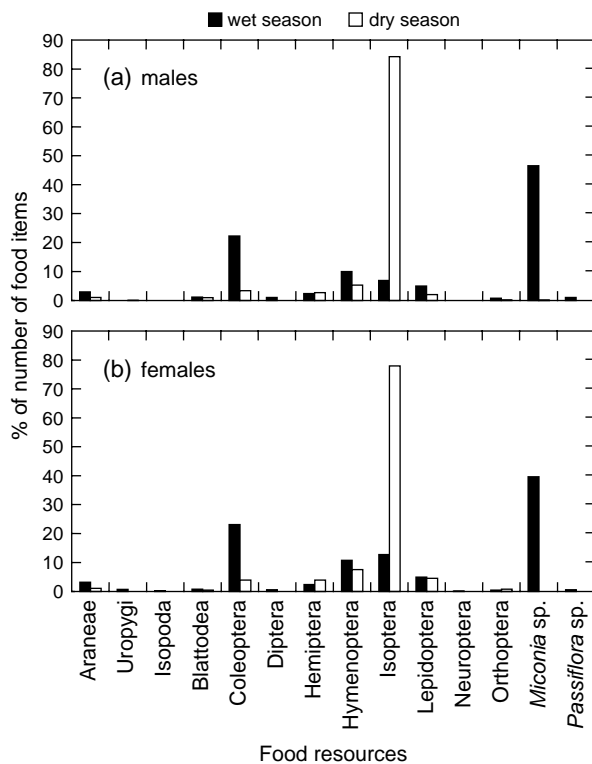


Figure 2. Diet composition as the percentage of the number of food items of male (a) and female (b) *Gracilinanus microtarsus* in the wet and dry seasons in a *Cerrado* remnant in Mogi Guaçu, southeastern Brazil.

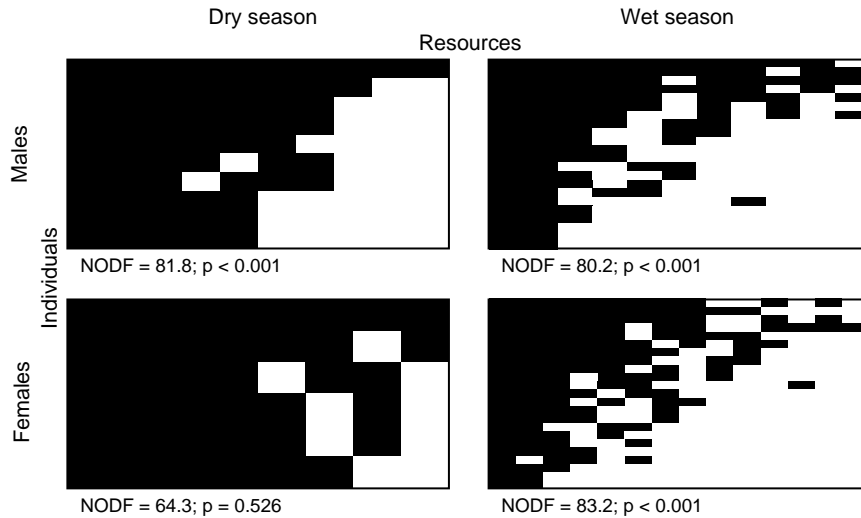


Figure 3. Matrices describing resource use by individuals for both sexes in different seasons. Black squares indicate that a given individual used a given resource. The measure of nestedness NODF varies from 0 (no nestedness) to 100 (perfect nestedness) and p-values lower than 0.05 indicate that the matrix is more nested than predicted by a theoretical model (see text for further details).

willingness to include the lower ranked resources in their diets. In such a scenario, for a given set of resources some individuals in the population would behave as generalists, while others would still specialize on the top ranked resources. More important, because rank preferences are the same for all individuals, they should add novel resources to their diet at a predictable order, causing nestedness. For example, if we assume that for one individual that ranks prey according to their energy (e) per unit handling time (h), $e_1/h_1 > e_2/h_2$ and for another individual $e_1/h_1 >> e_2/h_2$, it is easy to imagine that for a given level of resource abundance the former would include both resources in its diet, whereas the latter would still stick to resource 1 (Svanbäck and Bolnick 2005). As a consequence, the diet of the more specialized individual would be nested within the diet of the generalist.

The question remains on why phenotypic variation causes individuals to differ in the values they place to different resources. Differences in individual diet preferences are usually associated with functional tradeoffs that constrain an individual's ability to exploit different resources (Bolnick et al. 2003). For example, in the sea otter *Enhydra lutris*, exploiting different resources requires different behavioural skills that are both difficult to acquire and exceed the cognitive capacity of any single individual. As a consequence, once an individual learn how to exploit efficiently a given resource it tends to become specialized, and because individuals have different experiences they specialize on different resources (Estes et al. 2003, Tinker et al. 2007). *Gracilinanus microtarsus* uses different resources such as fruits, colonial insects (termites, ants) and highly mobile insects (e.g. beetles), which might demand different search/capture abilities. If the opossums need to learn where resources are and how to capture/handle them and there is a limit on how much information an individual can hold, this may cause diet variation. Alternatively, prey may have different digestive properties, imposing digestive tradeoffs. For example, yellow-rumped warblers *Dendroica coronata*, modulate their digestive

enzymes according to their diets, so that at any given time an individual is restricted to a particular digestive strategy and, therefore, can use some resources more efficiently than others (Afik and Karasov 1995). If individuals have different capacities to digest prey, prey may have different 'realized' energy contents to different individuals. These behavioural and physiological differences, by potentially changing individuals' search and handling times as well as the energy content of prey, might change their likelihood to add novel prey to their diets, making individuals to adopt different feeding strategies under similar conditions, as predicted by the 'shared preferences' model (Svanbäck and Bolnick 2005). Future studies should focus on measuring the energy content of the different resources used by *G. microtarsus* and most importantly the among-individual variation in their foraging skills and digestive abilities on different resources. We acknowledge that these ideas are rather speculative at the present time, but they provide testable hypotheses that would certainly help to identify the precise mechanisms causing diet variation and nestedness in this species.

We have documented another example that adds to a growing list of tropical species showing individual-level diet variation, including disparate taxa as frogs (Araújo et al. 2007, 2009), a hunting-wasp (Araújo and Gonzaga 2007), and lizards (Costa et al. 2008). This is relevant, because it is at odds with the prevalent view linking individual specialization to the invasion of 'empty' niches in depauperate, temperate communities (Skúlason and Smith 1995, Smith and Skúlason 1996). Moreover, we are documenting a novel pattern of resource partitioning at the individual level, namely nestedness, and providing a general framework that allows the investigation of intrapopulation patterns of resource use. It is still an open question how general this pattern is, but one of its implications is that if resources are limiting, competitive interactions among individuals will be highly asymmetric, which may affect the ecological and evolutionary dynamics of populations in ways that have yet to be determined.

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