BioSystems 118 (2014) 60–75

Contents lists available at ScienceDirect

BioSystems

journal homepage: www.elsevier.com/locate/biosystems

A new simplex approach to highlight multi-scale feeding behaviors in forager species from stomach contents: Application to insectivore lizard population

Nabil Semmar[a,b,*], Maurice Roux[b]

[a] Institut Supérieur des Sciences Biologiques Appliquées de Tunis (ISSBAT), Université de Tunis El Manar (UTM), Tunis, Tunisia
[b] Laboratoire de Biomathématiques, Service 462, Faculté des Sciences et Techniques de Saint-Jérômes, Avenue Escadrille Normandie Niemen, 13397 Marseille Cedex 13, France

ARTICLE INFO

Article history:
Received 5 July 2012
Received in revised form 20 February 2014
Accepted 27 February 2014

Keywords:
Foraging ecology
Nutritional trajectories
Dietary transitions
Memorization
Learning
Combinatorial approach
Geometrical approach
Simulation

ABSTRACT

Stomach contents represent complex mixture systems which depend on feeding mode and level of forager species (carnivores, herbivores) as well as on natural availability/distribution of food resources (preys, plants). Such mixture systems can be considered as small black boxes condensing wide ecological information on (i) feeding behaviors of predator (or herbivore) and (ii) local diversity of preys (or host plants). Feeding behaviors of a hunter species toward different prey taxa show a complex variability whose investigation requires multivariate statistical tools. This paper presents a new computational approach which statistically analyzes stomach contents' variability in a predator population to graphically highlight different feeding behaviors. It is a simulation approach iteratively combining the variability of different diet patterns by using a simplex mixture design. Average combinatorial results are graphically visualized to highlight scale-dependent relationships between consumption rates of different food types found in the stomachs. The simplex approach was applied on different subpopulations of *Phrynosoma douglassi brevirostre*, an insectivore lizard species. These subpopulations were initially defined by different criteria including statistical clusters, gender and sampling periods. Results highlighted successive trade-offs over months of captured potential preys switching from small and less mobile preys to large and flying ones. In these dietary transitions, *P. douglassi* manifested a systematic memorization of previous preys and a gradual foraging learning of the next ones. These results highlighted lightness on dietary flexibility helping this specialist predator to switch between diets based on different potential preys. Adult male and adult female lizards showed different feeding behaviors due to some predation lag-time between them and different dietary ratios toward the same considered preys.

1. Introduction

Modulation of feeding behavior as a function of prey or food type is a widespread phenomenon among vertebrates (Herrel et al., 1999; Anderson, 1993; Deban, 1997; Valdez and Nishikawa, 1997). Such modulation can find a deep fingerprint in foragers' stomach contents where different food types are mixed at different rates. By considering stomach contents as mixture systems, this paper focuses on the question of how a set of nutritional profiles can be statistically analyzed to highlight regulation mechanisms (feeding behaviors) governing diet variability in forager population? This question has both quantitative and qualitative aspects:

Under quantitative aspect, stomach contents can be expressed by relative levels (percentages) of different eaten preys (or plants). The different percentages constitute a diet profile from which preys' (plants') availabilities and foraging levels in consumer species can be estimated. Over time, variability between several stomach contents could provide fingerprint(s) on the dynamics of different food components (feeding levels' variations) in consumer species.

Under qualitative aspect, statistical analysis of relative variations between different food components (preys, plants, etc.) can help

Abbreviations: AbCtr, Absolute Contributions; ARA, Arachnida; CA, correspondence analysis; COL, Coleoptera; DIP, Diptera; DTr, diet trend; FOR, Formicidae; HCA, hierarchical cluster analysis; HEM, Hemiptera; HOM, Homoptera; HYM, Hymenoptera; LEP, Lepidoptera; OFT, optimal foraging theory; ORT, Orthoptera; SVL, snout-vent length.

* Corresponding author at: Institut Supérieur des Sciences Biologiques Appliquées de Tunis (ISSBAT), 9 Rue Zouhair Essafi, 1006 Tunis, Tunisia. Tel.: +216 71573721.
E-mail address: nabilsemmar@yahoo.fr (N. Semmar).

http://dx.doi.org/10.1016/j.biosystems.2014.02.003
0303-2647/

to highlight different feeding behaviors in the consumer species, i.e. food type preferences, dietary values of other food sources, transition mechanisms from a diet to another one, etc.

In stomach systems, mixed food components are inter-dependent and subsequently vary quantitatively the ones at the expense of the others. Such inter-dependences between relative levels of q components in mixture system are governed by simplex rules (Heiser, 2004; Kiyavash and Moulin, 2005; Raharjo et al., 2009; Bevilacqua et al., 2010): a simplex is defined as a space with $(q-1)$ dimensions in which q inter-dependent components vary the ones at the expense of the others (Figs. 1c and 2). This characteristic makes simplex spaces to be appropriate to statistically analyze regulatory processes controlling variability within mixture systems.

This paper presents a new computational simplex approach helping to understand how a forager species varies relatively its captured preys' levels to switch over different diet patterns. The approach combines the variability of different diet patterns to generate a dietary gradient from which multidirectional feeding behaviors can be highlighted in the considered predator species. The algorithm consists of six main steps: (1) classification, (2) combinations, (3) averaging, (4) iterations, (5) smoothing, (6) plotting.

(1) In a first step, the set of all the diet profiles are classified into homogeneous groups using statistical clustering criteria or discriminant biological/ecological factor(s). The resulting groups correspond to different forager subpopulations with different diet patterns. (2) After classification of all population individuals into some q groups, a simplex mixture design (Scheffé's matrix) is applied to combine the variability between and within these groups (Scheffé, 1958, 1963; Cornell, 1990). (3) Third, from the N combinations between the q groups, N average diet patterns are calculated in a response matrix. Subsequently, the mixture design provides a response matrix containing a complete set of gradual average diet patterns representing a multidimensional gradient between the q groups (q subpopulations). (4) In a fourth step, the mixture design and its response matrix are iterated k times by a bootstrapping technique to take into account the variability between and within the q groups. (5) Finally, the k resulting response matrices are averaged to obtain a single matrix containing N gradual smoothed diet patterns. (6) From the N smoothed diet patterns, scatter plots are visualized between relative levels of different food components (preys). In this graphical analysis, feeding behaviors of the q forager subpopulations are highlighted by considering their variable weights (given by the mixture design). For a given subpopulation, the successions of weights from minimal to maximal values highlight trajectories from which different scale-dependent feeding behaviors are identified toward different considered preys.

In this paper, the usefulness of the simplex approach to analyze feeding behaviors from stomach contents is illustrated by a specific example concerning a lizard population: a dataset of 45 individual food profiles of the insectivore lizard *Phrynosoma douglassi brevirostre* varying by relative levels of different arthropod preys (Powell and Russell, 1984; Linton et al., 1989; Manly, 2007). The flexibility of the simplex approach to analyze feeding behaviors is illustrated by two applications in which the studied population was initially classified according to two stratification criteria: (1) statistical type criterion defined from multivariate analysis and consisting of four clusters corresponding to four distinct diet trends; (2) biological type criterion combining gender with collect period leading to define four growth-maturity classes. After application of simplex approach, the different classes were separately considered to analyze their effects (roles) on feeding behaviors within the studied population. These behaviors implied foraging memorization and learning of successive potential preys with increasing body sizes and mobility levels. Bigger preys correlated with bigger (older) lizards. These results revealed to be compatible with the general contexts and principles of previously published models:

Optimal foraging theory (OFT) focuses on the flexibility of forager to exchange a previous advantageous food source by another one regarded as more desirable. Such dietary trade-off processes are governed, in forager, by optimization trends of benefit/cost ratios leading to higher energetic balances and lower preys' searching and/or handling times (Stephen and Krebs, 1986; Krivan, 1996; Charnov, 1976; Olsson and Brown, 2006). Other models studied the links between information acquisition process and foraging efficiency (Dall et al., 2005; Esposito et al., 2010; Nishimura, 1994). Also, some foraging models focused on the trade-off between the cost of harvesting information and the benefit of using it (Valone, 1989; Mangel, 1990; Eliassen et al., 2007). Alternatively to energy gain maximization raised by OFT, a large literature had emerged over the past few years demonstrating that animals (predators included) tend to obtain a diet that is balanced with respect to their nutrient requirements (Raubenheimer et al., 2009; Raubenheimer and Simpson, 2004; Jensen et al., 2012). Intake targets were shown to vary with the nutrient requirements which depend on different endogenous factors including levels of activity, growth and reproductive status of animal (Raubenheimer and Simpson, 1997).

2. Materials and methods

2.1. Studied population and background data

Studied population consisted of a data table (45 rows × 9 columns) containing proportions (x_{ij}) of 9 Arthropod types (preys) (j) found in the stomachs of 45 lizards (i) *P. douglassi brevirostre*. The nine prey types were: Ant or Formicidae (FOR), Hymenoptera (HYM), Homoptera (HOM), Hemiptera (HEM), Diptera (DIP), Coleoptera (COL), Lepidoptera (LEP), Orthoptera (ORT) and Arachnida (ARA). The lizard population was sampled near Bow Island in Alberta (Canada) at four successive months (June–September 1980) (Powell and Russell, 1984). The inventory data were originally published by Linton et al. (1989) then by Manly (2007).

The 45 lizards belonged to two body size classes including adult males/yearling females on one hand, and adult females (larger) on the other hand (Manly, 2007). The sampling was balanced neither between months nor between body size classes: the 45 samples were distributed between (3, 6), (5, 6), (10, 3) and (6, 6) of (adult males/yearling females, adult females) in June, July, August and September, respectively. Younger individuals usually died after gut flushing (Powell and Russell, 1984).

Under methodological aspect, the 45 stomach contents were obtained by a serial of capture–recapture of lizards over the four successive months in four-five short sampling periods (each of 2–4 days). After gut flushing by a stomach pump and a short recovery period, the lizards were released at the capture site. Moreover, further information about arthropod species composition was gathered using pitfall traps (Powell and Russell, 1984).

2.2. General principle of combinatorial simplex approach

Starting from q separated groups (Fig. 1a) defined by a statistical or a biological criterion, one could ask about how did food profiles vary to favor the emergency of well distinct diet patterns characterizing the q studied subpopulations? Under structural aspect, this question is closely linked to the variability of feeding behaviors between and within different lizard groups. Under functional aspect, these groups could be considered as q feeding poles