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# A statistical social network model for consumption data in trophic food webs



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## ABSTRACT

We adapt existing statistical modeling techniques for social networks to study consumption data observed in trophic food webs. These data describe the feeding volume (non-negative) among organisms grouped into nodes, called trophic species, that form the food web. Model complexity arises due to the extensive amount of zeros in the data, as each node in the web is predator/prey to only a small number of other trophic species. Many of the zeros are regarded as structural (non-random) in the context of feeding behavior. The presence of basal prey and top predator nodes (those who never consume and those who are never consumed, with probability 1) creates additional complexity to the statistical modeling. We develop a special statistical social network model to account for such network features. The model is applied to two empirical food webs; focus is on the web for which the population size of seals is of concern to various commercial fisheries.

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## 1. Introduction: food webs as social networks

A food web is a network of organisms and what they consume. When the relationship among these is of interest, organisms (inanimate or otherwise) are typically aggregated at various resolutions to form *trophic species*. For example, one trophic species in a given web may consist of various types of organic dead matter collectively referred to as detritus, while another in the same web may consist of

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the single anole species *A. gingivinus*. We refer to a trophic species as a food web *node*. In the trophic context, feeding relations among nodes are of interest. (In contrast, the ecosystem context of a food web concerns the closed-loop transfer of energy and nutrients [1,2,4,25].) Thus, trophic food web research concerns the understanding of the interdependency, or network structure, among trophic species with respect to predation or consumption behavior.

For a given pair of nodes ( $i, j$ ), the four possible within-pair trophic relations are depicted as

$$i \quad j \quad i \rightarrow j \quad i \leftarrow j \quad i \leftrightarrow j \quad (1)$$

where, conventionally, any link/edge points from prey to predator. From left to right in (1), the depictions respectively represent no predation between  $i$  and  $j$ , predation of  $i$  by  $j$  but not *vice versa*, predation of  $j$  by  $i$  but not *vice versa*, and mutual predation between  $i$  and  $j$ . To represent (1) in a quantitative framework, “ $i \quad j$ ” consists of two zero links, each of “ $i \rightarrow j$ ” and “ $i \leftarrow j$ ” consists of a zero and a positive link, and “ $i \leftrightarrow j$ ” consists of two positive links. Thus, each pair ( $i, j$ ) yields two directed links: from  $i$  to  $j$ , and from  $j$  to  $i$ . Extending this to all  $n$  nodes in the food web, we have a network that consists of  $2 \times (n\text{-choose-}2) = n(n-1)$  pairwise or *dyadic* directed links. Presence and absence of feeding interactions are represented by binary links, while consumption volumes are represented by non-negative *weighted* or *valued* links. A binary link qualitatively describes the pairwise relation, while a weighted link reflects the degree of one node’s dominance over the other. Thus, binary and weighted links yield different insights into the network structure.

Research on network structure arises in many practical settings, commonly in the social sciences, e.g., pair bonds [19], international trade and militarized disputes [29,31]. Many quantitative social network analysis (SNA) techniques have been developed to understand network relational patterns [22,30], and some, adopted in food web research [7,17]. These earlier SNA methods for food webs were largely based on the mathematical notion of equivalence class for defining congruence among individual elements in a given set according to certain criteria (see, e.g., [9]); the objective is to seek optimal partitions of the network into compartments of nodes subject to the given criteria. For example, compartments identified in a food web may correspond to trophic levels. Chiu [3] overviews some common SNA techniques for food web research.

Statistical approaches for SNA began more than half a century ago [12], but research interest and methodological advancement in the area grew dramatically in the past two decades, due in part to the exponential increase in computational technologies and the general public’s interest in social networks. In particular, statistical regression methodologies were developed only recently to express network links  $y_{ij}$  as the random response of within-node and inter-node characteristics [11,14,15, 28,31]. The resulting conclusions about network features are purely empirical and entirely based on observed network attributes without the use of network dynamics or subject-matter theory. Chiu and Westveld [5] demonstrate that, in the context of binary food webs, taking a statistical SNA approach can provide an alternative perspective of trophic relational patterns according to feeding activity and preference. These authors adapted the statistical SNA latent-space modeling framework by Hoff [14] and Ward et al. [29] to regress the presence–absence of pairwise predation, in a mixed-effects logistic model, on the dyadic characteristic of phylogenetic similarity; eight food webs were analyzed this way. The basis of their statistical model for SNA is a two-way analysis-of-(co)variance (ANO(CO)VA) model (see Section 2).

Chiu [3] and Chiu and Westveld [5] discuss the various advantages of using this statistical SNA framework to study food webs, most notably: The inherent uncertainty in network links is readily acknowledged and modeled by the framework; in addition to “Who tends to eat whom?” the model can address “Why?” through covariates, avoiding post-SNA “detective work” that is typical of conventional SNA methods; rigorous quantitative inference (including predictive inference) can be made for various features of feeding behavior, from food web connectance to the relative distinction among nodes with respect to consumption activity level and preference; and finally, all these can be achieved through a single unified statistical analysis through the regression framework, thus avoiding the intractable propagation of uncertainty in conventional multi-step analyses.

These merits are true for  $y_{ij}$  in general, i.e., for binary or weighted data ( $y_{ij} \geq 0$ ). However, weighted food web data often pose a modeling challenge, due to the high incidence of  $y_{ij} = 0$ . For example, each of the eight food webs analyzed in [5] consists of between 69% and 98% zeros. Direct application

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