A methodology to quantify the long-term changes in social networks of competing species

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A B S T R A C T

Current methods of social network analysis need detailed data, which are often unavailable for long periods of time (e.g. decades). The main objective of the present work is to develop and test a methodology that requires less detailed data and relies on user-defined mathematical models. This methodology is a three-step procedure described as follows. First, long-term population data is divided into n subsets based on the desired time unit (e.g. months, or years). Second, a class of mathematical models are defined and fitted to each subset of data, where growth, migration, and interaction parameters are estimated. Third, time series of estimated parameter values are analyzed to detect trends, periodic cycles and patterns of ecological dominance. To examine the robustness of this method, the annual competitive Lotka–Volterra (CLV) models were parametrized using the long-term (1973–2003) population densities of five rodent species residing in Kansas: cotton rat (CR), prairie vole (PV), white-footed mouse (WFM), deer mouse (DM), and western harvest mouse (WHM). Using the Fourier series models fitted to the estimated parameter values, we found that the periodic cycles of growth and competition rates were about 5.5 and 11 years for CR and about 2.6–3.8 years in all rodent species. The linear regression models fitted to the estimated values indicate slight decreases in the growth rates of all species except PV. The competing effects of PV on CR and WFM have decreased more than 11.4%. Whereas the competing effect of the DM on PV, and WFM on DM and itself have increased by 15.4%, 25.8% and 14.9%, respectively. The estimated migration rates of DM and WHM were mainly negative, which indicates that these species were mainly migrating out of the study site. All other three species had mainly positive migration rates. The parametrized annual CLV models were employed to analyze the formation of stable equilibria and to numerically investigate spatio-temporal patterns of population densities. We found that CR and PV were often dominant. The present work is the first step towards employing user-defined models compensating for the lack of long-term detailed social network data.

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1. Introduction

Social network analysis has been much appreciated for revealing causes and consequences of various interactions within and between wildlife communities (Bascompte, 2009; Krause et al., 2009; Wey et al., 2008). This includes social network analysis of inter- and intra-specific competitions and their subsequent impacts on the population dynamics of interacting species (Araujo et al., 2008; Haulsee et al., 2016; Fisher et al., 2016). Despite being a promising tool, there is currently no pertinent methodology for measuring long-term changes in the social networks of interacting species. This is mainly due to lack of long-term (e.g. decades) detailed network data, which is a major challenge in quantifying the long-term network dynamics of interacting species. In particular, the current statistical methods (Allesina and Levine, 2011; Bronstein, 2009; DuBowy, 1988; Fisher et al., 2017) require detailed network data, which are often unavailable for long periods of time. Unpacking wildlife social networks of species (Bascompte, 2009; Krause et al., 2009; Perkins et al., 2009; Shizuka and McDonald, 2012; Wey et al., 2008) has been mainly limited to short-term study periods.

There is a critical need to develop a new methodology that requires less detailed data and it is capable of assessing the long-term dynamics of social networks (e.g. periodic cycles, trends, seasonality, and ecological dominance). For instance, several long-term trapping records of interacting species are available for a

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variety of interacting species. These records can be used to obtain long-term estimates of population densities. As shown in the present work, these estimates can serve as less detailed but available data. The main objective of the present work is to develop and test a methodology that requires less detailed data for analyzing long-term dynamics of wildlife social networks. This methodology relies on user-defined mathematical models which compensate for lack of detailed network data. In particular, if the type of interactions between and within species is known (e.g. facilitation, competition, prey-predator), then details of the data related to that type of interaction in no longer necessary and the user can directly define them in the mathematical models. Therefore, the user-defined models can be fitted to the long-term population estimates to quantify the dynamics of wildlife social networks. The present work proposes a new methodology that can be utilized to obtain a deeper understanding of the ecology of interacting species.

A mathematical model is built based on certain assumptions related to the social network. These assumptions play a key role in the model formulations. If the assumptions are widely accepted, then the model outcomes can detect and quantify several ecological phenomena present in the wildlife community. A class of well-studied mathematical models is known as Lotka–Volterra (LV) models. In particular, a spatially homogeneous network of n interacting species with densities $y_i(t)$ is modeled by the following LV model

$$\frac{dy_i(t)}{dt} = r_i y_i(t) \left(1 - \frac{\sum_{j=1}^{N} \alpha_{ij} y_i(t)}{k_i} \right), \qquad (1)$$

where the positive constant r_i is the population growth rate of species i, k_i is the carrying capacity of species i, $\alpha_{ii} = 1$ and α_{ij} (with $i \neq j$, $1 \leq i, j \leq n$) is the interacting effect of species j on the population of species i.

Model (1) has frequently been used by ecologists and analyzed by mathematicians for several decades (Geijzendorffer et al., 2011; Gyllenberg et al., 2006; Gyllenberg and Yan, 2009; Knebel et al., 2013; Lian et al., 2008). An *n-dimensional* LV model represents the dynamics of n interacting species. It is known that a two-dimensional LV model cannot admit isolated periodic orbit (Hofbauer and Sigmund, 1998); that is, if the system has periodic orbits, then these orbits are non-isolated. The higher dimensions of the LV model exhibit rich dynamics.

In an LV model of n interacting species, the user may define certain type of interaction (e.g. facilitation, commensalism, or competition) between each pair of species. In the present study we consider the competitive Lotka–Volterra (CLV) model (Hofbauer and Sigmund, 1998; Zeeman, 1993; Zhaoa et al., 2009), which assumes that the social network structure of interacting species is based on the continuous competitions within and between the species. The three-dimensional CLV model with no periodic orbits has been analyzed by Van Den Driessche and Zeeman (1998). Specifically, there will be no coexistence and one of the species will out-compete the other two, when each species resists invasion from the other two at carrying capacity. On the contrary, there will be a coexistence when none of the species can resist invasion from the others. Theoretical studies of the CLV model includes the outstanding work of Zeeman (1993), where she used geometric analysis of the surfaces to define a combinatorial equivalence relation by inequalities on the parameters of model (1). Then a classification of 33 stable equivalence classes for the three-dimensional CLV model was deduced. Zeeman showed that 25 classes correspond to equilibrium solutions and the other 8 cases represent

periodic solutions via Hopf bifurcations. For 27 of these classes, the dynamical behaviors of the systems have been fully described (Van Den Driessche and Zeeman, 1998; Zeeman, 1993). Classes 26–31 can possess isolated periodic orbits or limit cycles. The question of how many limit cycles can appear in Zeeman's six classes 26–31 is still open. Conditions for extinction of species have been established in Theorem 2.1 of Zeeman (1995). Previous studies (Hofbauer and Sigmund, 1998; Lu and Luo, 2003; Gyllenberg et al., 2006; Gyllenberg and Yan, 2009; Lian et al., 2008) show that there is only a finite number of limit cycles, where up to four limit cycles have been discovered. However, these limit cycles have not been numerically explored in details.

The above-mentioned dynamics of model (1) indicate that the parameters of the model can measure and unpack the complex nature of social networks within and between species. Here, the main objective is to develop and examine a methodology that employs model (1) to identify factors such as trends and periodic cycles in the growth rates, migration, and levels of interactions within and between the species. These factors characterize the long-term dynamics of social networks and govern the observed changes in the population densities of interacting species.

Given the ecology and characteristics of certain species, it is reasonable to assume that they compete for the same food resources available in the environment. Then using CLV models to analyze the social interactions of these species seems rational. As explained in the next section, we used long-term data of five competing rodent species to test the robustness of CLV models and to quantify the long-term annual changes in the rates of populations growth, competitions, and migrations. These changes are characterized by times series analysis of the estimated parameter values of the annual CLV models. The time series analysis can provide explanations for extinction, dominance, trends and synchronized oscillations in the population densities. Although the primary focus of this paper is to develop a methodology and measure long-term changes in the social networks of rodents, the parametrized CLV models can also be used to numerically investigate the spatial variations in the population densities of rodent species. In particular, by including a diffusion term into the CLV models, we numerically explored the coexistence, dominance and spatio-temporal patterns of population density occurring in the study area during the years 1973–2003.

2. Materials and methods

The proposed methodology consists of three main steps: (i) dividing the long-term population data into n subsets of population data based on the desired time unit (e.g. weeks, months, or years); (ii) fitting the competitive Lotka–Volterra (CLV) models to each subset of data to extract the time series of estimated growth, migration, and competition rates; (iii) using statistical models (i.e. linear regression and Fourier series models) to analyze the time series of the estimated values and to measure periodic cycles, trends and synchronized patterns of population variations occurring over long periods of time.

2.1. Study site and rodent data

We used 31 years of monthly trapping records (August 1973–July 2003) of rodents to estimate the proportional population densities of rodents residing in the study site. These estimates were used to specify annual CLV models and to identify long-term patterns of inter- and intra-specific population interactions. The five rodent species consist of hispid cotton rat (*Sigmodon hispidus*), prairie vole (*Microtus ochrogaster*), deer mouse (*Peromyscus maniculatus*), white-footed mouse (*Peromyscus leucopus*), and western