Environmental variability and density dependence in the temporal Taylor's law

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ABSTRACT

Taylor's law (TL) is an empirical rule describing the approximate relationship between the variance and the mean of population density: $\log_{10}(\text{variance}) \approx \log_{10}(a) + b \times \log_{10}(\text{mean})$. Although TL has been verified in various ecological systems, essential questions remain unanswered. Why is TL so widely observed? What mechanisms or processes generate TL? Why do most observed slopes b fall in the limited range $1 < b < 2$? Density-dependent movement of individuals among populations has been proposed as a mechanism that leads to TL with slopes $1 < b < 2$. We used the Gompertz model (a second-order autoregressive model of the logarithm of population density) to analyze the temporal TL of gray-sided vole populations. Our extensive simulations using various combinations of model parameters for environmental variability and density dependence demonstrated that sustainable populations could obey TL in the absence of density-dependent movement among populations, and identified the parameter combinations that produced slopes $1 < b < 2$. When environmental variability was low and density dependence was intermediate, simulated data sets showed higher probabilities for $1 < b < 2$, but the probability was not very high. In general, slopes became steeper (b increased) as environmental variability increased and as density dependence coefficients decreased. In the Gompertz model, both environmental variability and density dependence cause population density to vary, and on the logarithmic scale of population density, those effects are symmetric above and below the equilibrium density. However, effects of the variability are higher above the equilibrium density on the natural scale of population density, and thus the mean of population density increases with increasing population variability. Therefore, the temporal TL can be formed when population density is measured in the natural scale. In sustainable populations well described by the Gompertz model, the slope b can be determined by the interplay of environmental variability and density dependence.

1. Introduction

Taylor's law (TL, Taylor, 1961) is an empirical rule describing the approximate relationship between the variance and the mean of population density. It has been widely verified in various ecological systems (Taylor, 1986) and many other fields (Eisler et al., 2008; Tippett and Cohen, 2016). TL asserts that the variance is approximately a power-law function of the mean: variance $= a \times (\text{mean})^b$, $a > 0$. It is usually rewritten:

$$\log_{10}(\text{variance}) = \log_{10}(a) + b \times \log_{10}(\text{mean}). \tag{1}$$

Neither of these equations specifies the deviations from an exact relationship, i.e., the error term in TL.

The mean and the variance of population density can be calculated temporally and spatially. In the temporal TL, the mean and the variance are calculated over observations of population density at different times in a given location, while in the spatial TL, the mean and the variance are calculated over observations of population density in different spatial locations at a given time. The temporal mean of population density may depend primarily on habitat quality, while the temporal variance of population density may be produced primarily by population dynamics in interaction with environmental variable factors, which broadly include abiotic (e.g., climatic, chemical, physical) and biotic (e.g., trophic, parasitic, allelopathic) effects on a given species. This study investigated the relative contributions of population dynamics and environmental variability in shaping the form and parameters of the temporal variance-mean relationship.

Many theoretical models and interpretations of TL have been proposed, but none has gained widespread acceptance. Essential questions remain unanswered. Why is TL so widely observed? What mechanisms or processes generate TL? Why do most observed slopes satisfy $1 < b < 2$? Although combined empirical and theoretical studies should be conducted to answer these questions, many previous empirical studies have verified TL without testing the details of any model that leads to TL, while theoretical models that lead to TL have often lacked detailed empirical verification of the processes assumed (see reviews by Taylor, 1986; Kendal, 2004; Eisler et al., 2008, but as exceptions see Cohen et al., 2013; Linnerud et al., 2013).

We found previously that the population density of the gray-sided vole, *Myodes rufocanus* (Sundevall, 1846), in Hokkaido satisfied the temporal TL, and the estimated slope 1.613 was in $1 < b < 2$ (Cohen and Saitoh, 2016). Moreover, Cohen and Saitoh (2016) showed that the densities of different vole populations were not independent. The Gompertz model, which describes well the dynamics of the logarithm of population density of those populations (Royama, 1977, 1992; Stenseth, 1999; Stenseth et al., 2003), generated time series of density on the original scale of measurement that satisfied the form of temporal TL, but, under the assumption that different populations were independent, the slope $b \approx 2.699$ of the simulated TL was significantly steeper than the slope of the empirical populations. We attributed this discrepancy to the assumed independence of simulated time series.

In contrast to the independent simulated time series, empirical populations may inhabit habitats of varying quality, may be subject to correlated environmental influences (the "Moran effect"), and may experience density dependent movements from a higher-quality habitat to a lower-quality habitat. Density-dependent movement reduces the temporal mean and variance of populations in higher-quality habitats, while it enhances the temporal mean and variance of populations in lower-quality habitats. Therefore, density-dependent movements could lower the temporal slope of TL, as Taylor and Taylor (1977) and Perry (1988) suggested. Synchrony of populations produced by the Moran effect could also lower the slopes of the spatial TL (Reuman et al., 2017).

Density-dependent movements, however, seem unrealistic for the studied vole populations, because the distance between the studied vole populations is far beyond the movement ability of individuals of the gray-sided vole. The mean geographic distance between the observed populations was 8.4 km, while most natal dispersals of individuals are recorded within several hundred meters (Ishibashi and Saitoh, 2008), although some long-distance movements of up to several kilometers have been reported in some arvicoline rodent populations, which are highly variable (see Le Galliard et al., 2012 for a review). Therefore, we shall test whether TL can be formed, with realistic values of the slope parameter b, even in the absence of demographically significant migration.

Here we report detailed simulations of the temporal TL for the empirical populations of the gray-sided vole using the Gompertz model with extensive combinations of model parameters. These results will shed light on the above general questions about TL in this situation.

Modelling of population dynamics is a powerful approach to simulating observed populations, analyzing effects of model parameters, and considering underlying mechanisms of the temporal TL. Anderson et al. (1982) proposed a Markovian population model where chance demographic events could lead to the temporal TL by the adjustment of the relative rates governing birth, death, immigration, and emigration. Perry (1988) demonstrated that models based on density-dependent movement could yield the temporal TL. Hanski and Woiwod (1993) simulated populations where the intrinsic growth rate of populations was subjected to a random component; these simulated populations approximated the temporal TL. All of these attempts, however, relied upon arbitrary approximations, transformations or constraints to achieve the goal (Kendal, 2004). In addition, the models of population dynamics used by those studies were not tested to evaluate whether they could describe empirical populations well, and some models were

unrealistic. For example, Anderson et al. (1982) assumed a potentially infinite increase of population density, and Perry (1988) assumed density-dependent movement that is unrealistic, at least for the studied populations of the gray-sided vole.

Linnerud et al. (2013) analyzed density dependence and stochastic effects on the temporal TL using empirical data on avian populations and modified logistic models. They claimed that slopes of the temporal TL were influenced by interspecific variation in life history parameters (adult survival and clutch size). However, their examined parameter space of population dynamics was limited. In contrast, Royama (1977, 1992) examined the relationship between the density-dependence coefficients and the population dynamics of the Gompertz model (details below) and identified the parameter space of density-dependence coefficients where populations are sustainable (mathematically speaking, where the second-order autoregressive model is stationary and ergodic). Therefore, we can thoroughly analyze effects of density dependence on the temporal TL for sustainable populations using the Gompertz model with fewer arbitrary approximations or assumptions.

Here we will show, first, that the variability of population density derives from both environmental variability and density dependence. Second, by extensive analyses of environmental variability and density-dependence coefficients without assuming density-dependent movements or environmentally caused synchrony, we will show that sustainable populations satisfy the temporal TL and will identify parameter combinations that are more likely to produce slopes $1 < b < 2$. Further, we will show that a driving force of the temporal TL formation is population variability but not the variation of the equilibrium density.

2. Materials and methods

2.1. Study design and data

Hokkaido is the northernmost island of Japan (78,073 km^2). The gray-sided vole, *Myodes rufocanus* (Sundevall, 1846), is the commonest species of rodents on this island (Kaneko et al., 1998). A systematic survey of rodent populations has been carried out in Hokkaido by Forestry Agency of Japanese Government. The geography of Hokkaido and the data collection were described previously (Saitoh et al., 1997, 1998; Stenseth et al., 2003). We analyzed the same data set of the gray-sided vole as Cohen and Saitoh (2016): $N = 85$ populations in different locations covering $T = 31$ years (1962–1992). Population density was defined as the number of voles per 150 trap-nights, because 50 snap traps for three consecutive nights on a 0.5 ha survey plot was a standard unit of the rodent survey.

The Bayesian method was applied to the estimation of population density for each year and location based on a state-space model by using WinBUGS version 1.4.3 (Spiegelhalter et al., 2003, http://www.mrc-bsu.cam.ac.uk/software/bugs/). In our previous study (Cohen and Saitoh, 2016), population density was estimated assuming that the number of voles caught increased in proportion to trapping effort. However, there were some limitations imposed by the trapping method. Because the basic unit of trapping was 150 trap-nights, the number of catches could not exceed 150 per unit. New codes for WinBUGS were developed taking the constraints of trapping into consideration. In addition, non-target species of rodents (*Apodemus argenteus, A. speciosus,* and other minor species) than the target species (*Myodes rufocanus*) provided some small proportion of caught rodents, although the target species dominated other species (Saitoh and Nakatsu, 1997). Traps occupied by other species should not be considered effective traps. Therefore we subtracted the number of catches with non-target species from the number of trap-nights. The new codes for WinBUGS are available as Appendix B in Supplementary Material. The raw counts of voles trapped, the trapping effort (the total number of trap-nights, excluding traps occupied by non-target species), and the resulting Bayes population estimates are available in a spreadsheet file as Appendices H–K.