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Taylor's Power Law as a Consequence of Fretwell's Ideal Free Distribution

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In field studies of population density, variance often increases as a power function of the mean. This empirical relationship has been formalized as Taylor's Power Law (TPL: Taylor, 1961), which has been used to quantify aggregation and to transform data for statistical analysis. Habitat selection theory suggests that animals will match population density to resource availability such that all individuals have equal rates of resource gain. This pattern, known as an "ideal free distribution" (IFD: Fretwell & Lucas, 1970) has been found in many field and laboratory investigations. Here we demonstrate that when animals form an IFD, the variance among census samples must increase as the square of the mean density. This result closely matches the mean value of 2·1 for the exponent of TPL derived from 444 studies of individual bird and insect populations (Taylor *et al.*, 1983). We suggest that TPL results from resource tracking by animal populations. Deviations from the exponent of 2 are readily explained by density-dependent changes in resource defence, interference and risk of predation. Both demographic and behavioural mechanisms have been previously suggested as potential causes of TPL. We show that attempts to distinguish between demographic and behavioural mechanisms using simulations are unreliable because their results may depend more upon the statistical properties of the simulated environment than upon the processes controlling dispersion. Demographic events are the most probable causes of TPL when sampling programs cover several populations, but behaviour is probably the mechanism within a population of motile animals. The exponent of TPL is a poor comparative index of aggregation, because many different levels of spatial aggregation can lead to an exponent of 2.

Introduction

Animals live in environments in which resource levels can vary widely through space. Habitats can be defined as regions of similar resource availability within these environments (Fretwell & Lucas, 1970; Fretwell, 1972). If individuals' foraging rates are directly proportional to local resource levels and inversely proportional to competitor density, at equilibrium, the proportion of the population in a habitat should equal the proportion of resources in that habitat (Maynard Smith, 1982). This pattern was named the "ideal free distribution" (IFD) by Fretwell & Lucas (1970) because of its theoretical dependence upon "ideal" knowledge of and "free" access to all habitats. Subsequent theoretical and empirical studies have shown that the IFD can occur even when these conditions are violated (Whitham, 1980; Harper,

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1982; Milinski, 1984; Godin & Keenleyside, 1984; Regelmann, 1984). Most studies using the IFD model have focused on predicting the mean density within habitats at a single population size. However, the IFD also has implications for the variance among samples from different habitats.

The variance of density estimates plays a major role in ecological studies. Relationships between the mean and variance of sample counts in field data generally follow a consistent pattern, which has been formalized as Taylor's Power Law (TPL: Taylor, 1961). TPL relates the mean and variance among census samples by the expression

$$S^2 = a\bar{X}^b \tag{1}$$

where a and b are empirically fitted constants. The exponent has been used as an index of aggregation (random $b = 1$, aggregated $b > 1$, approaching uniform $b < 1$) while variation in the constant a has been attributed to sampling techniques (Southwood, 1978).

Several models have attempted to explain the power relationships between mean and variance using both behavioural (Taylor & Taylor, 1977) and demographic (Hanski, 1980; Anderson *et al.*, 1982) mechanisms. Such models may generate virtually any value of b, depending on the values of model parameters. In this paper we shall show that the IFD leads to a version of TPL with biologically reasonable values of b, using parameters that can be measured independently of the distribution data.

The Model

We begin our derivation by considering an environment composed of several habitats which are characterized by differing resource renewal rates (Fretwell, 1972). Samples from such an environment are likely to come from different habitats, though the spatial heterogeneity of resources may not be apparent to those conducting the study (Whitham, 1980). We assume that the ratio of renewal rates among habitats, the area of the habitats and their number does not change through time. Later we will discuss how deviations from these assumptions can affect our conclusions. The variance of the number of individuals in a sample is estimated as

$$S^2 = \sum \frac{(X_i - \bar{X})^2}{(n-1)} \tag{2}$$

where $\bar{X}$ is the mean value, n the number of samples taken, and the summation refers to all samples. According to TPL, the variance S^2 will be related to the mean $\bar{X}$ through equation (1). The IFD predicts that the expected proportion of the population in a census sample from a particular habitat will be proportional to the habitat's relative resource renewal rate. The formula for sample variance can also be expressed in terms of the fraction $X_i/\bar{X}$ as follows

$$S^2 = \bar{X}^2 \sum \frac{((X_i/\bar{X}) - 1)^2}{n-1}. \tag{3}$$

Having defined the variance as the product of the two quantities on the right-hand side (the square of the mean, and the summation), we can see that the expected value of the variance will be equal to the product of the expectations of these two quantities

$$E(S^2) = E(\bar{X}^2) \, . \, E\left\{\frac{\sum((X_i/\bar{X}) - 1)^2}{n-1}\right\} \tag{4}$$

if and only if $X_i/\bar{X}$ is a constant for all samples i. This, however, is precisely the property of the IFD: for example, a doubling of the mean density will simply double the density at all sites. Therefore, equation (4) holds and (1) and (3) are equivalent, with $b = 2$ and

$$a = \sum \frac{((X_i/\bar{X}) - 1)^2}{n-1}.$$

We shall refer to the estimates of the TPL parameters derived from the $X_i/\bar{X}$ values as β and α, while b and a will refer to values estimated by regression of sample means and variances in the manner originally proposed by Taylor (1961). α explicitly represents the heterogeneity of animal densities among samples scaled by population density, and reflects the resource distribution of animals which follow the IFD. The b of TPL will equal 2 when animals form IFDs in an unchanging environment. More generally, b will equal 2 for animals following the IFD among a set of sample sites whenever α (the heterogeneity of $X_i/\bar{X}$ among samples) remains constant, regardless of changes in the values of $X_i/\bar{X}$ in any particular sample through the study. Randomly relocating samples across the environment studied during each population estimate should not bias α as, on average, all habitat types will be equally represented among the samples.

The prediction that $b = 2$ when the IFD is satisfied is in remarkable agreement with the latest and most extensive account of the TPL: Taylor *et al.* (1983) find that the average value of b is 2·1 (standard deviation 0·4) among 444 species of birds, aphids and moths. It is on this basis that we propose the Ideal Free Distribution as an explanation of observed variance-mean relationships.

The Effect of Varying α

Changes in the environment, or animals responses to it, which alter the distribution of $X_i/\bar{X}$ values among the samples will be reflected by variation in α. As the animal distribution becomes more regular across the environment, the value of α approaches 0. α may vary for a number of reasons. For example, the environment may be changing over the time of the study (Taylor *et al.*, 1983). However, in order for such changes to have an effect on animals which follow the IFD, habitat areas and/or relative qualities would also have to change; their relocation in space is not enough. Also, random fluctuations in α will not affect the expected estimate of b. Only variation in α correlated with changes in $\bar{X}$ will result in exponents which differ from 2. A potential cause of a correlation between α and $\bar{X}$ is changing interactions among individuals as population density increases.

The Effects of Behavioural Responses to Density on TPL

The IFD has lead to the development of other behavioural models: the Allee-type IFD, the ideal despotic distribution and the interference IFD (Fretwell, 1972; Gillis & Kramer, in prep.), which deal with situations where individual interactions do not follow the initial IFD assumptions. The occurrence of these alternative patterns can be affected by population density, resulting in empirically derived *b* values less than and greater than 2.

The benefits of high animal density for foraging rate and survival may lead to aggregation (Hamilton, 1971; Pulliam, 1973; Magurran & Pitcher, 1983). The potential for improved foraging in groups was recognized by Fretwell (1972) and developed further by Pulliam & Caraco (1984) as the Allee-type IFD. In this distribution more animals gather in the best habitats than would be expected from resource levels due to the benefits of increased group size. Recent studies suggest that this effect is only significant at low population density (Elgar *et al.*, 1984). Allee effects can cause increased variation in the values of $X_i/\bar{X}$ among samples at low densities, resulting in higher α's. However, as $\bar{X}$ increases, the mean density in all habitats will become large and the pressure to join the largest group will disappear. The values of $X_i/\bar{X}$ among the samples will become more regular and α will decrease. This can result in an empirically derived *b* which is less than 2 due to the greater variance at low densities.

Resource defence by despotic individuals may result in fewer individuals than expected in the better habitats. This is the ideal despotic distribution (Fretwell, 1972; Ens & Goss-Custard, 1984; Talbot & Kramer, 1986). In this case α will differ from the IFD prediction due to aggressive behaviour. However, resource defence is expected to be more common at low densities according to the principle of economic defendability (Brown, 1964), which suggests that defence should decrease as intruder pressure increases. A pattern of decreasing agonistic activity with increasing density has been observed in the field (Sale, 1972; Jones, 1983). This could result in a switch from the ideal despotic distribution to the IFD as density increases. In very heterogeneous environments, the value of α associated with the IFD will be greater than the α resulting from ideal despotic distributions, and can cause *b* to be greater than 2. Conversely, in more homogeneous environments the ideal despotic distribution may generate more variance among samples than expected from the IFD, possibly resulting in *b* values less than 2. The magnitude and direction of the observed trend will depend upon the behaviour of the animals in the specific environment studied.

Interference IFD's (Gillis & Kramer, in prep.) can form at high densities if individuals avoid the better patches due to reduced foraging rates brought about by the presence of conspecifics. A "reversible, short term reduction in foraging rate" due to the local forager density is termed interference (Goss-Custard, 1980) and has been observed in both field and laboratory studies (Ens & Goss-Custard, 1984; Hassel & Varley, 1969). Interference affects the relationship between animal and resource distributions (Sutherland, 1983) and may result in decreasing variation in animal numbers among habitats as density increases in heterogeneous environments

(Gillis & Kramer, in prep.). The trend of decreasing α with increasing $\bar{X}$ will cause the empirically derived b to be less than 2.

Relevance of the IFD to Other Models

The patterns described as a result of the IFD and other behavioural mechanisms can also be generated by more complex models (Taylor & Taylor, 1977; Hanski, 1980; Anderson *et al.*, 1982). Hanski (1980) objects to Taylor's delta-model (Taylor & Taylor, 1977) on the grounds that it depends on non-random migration to track resources over areas which are large relative to the mobility of the organisms involved, and suggests that it is really a restatement of the IFD. Though Taylor's delta-model results in the same patterns as the IFD through directed migration, it is nevertheless a distinct model. In the delta-model, migration between sites is based upon a single response to local density which is independent of local resources. This conflicts with the IFD where movement is related to local density and resource levels. Furthermore, some of the delta-model's parameters are defined as having "no biological interpretation" (Taylor & Taylor, 1977: p. 419) while the IFD parameters are defined in terms of the organism and its environment (Fretwell, 1972).

Demographic models (Hanski, 1980; Anderson *et al.*, 1982) with random migration between sites can generate the same result as the IFD. Even the potential deviations from the IFD caused by interference and facilitation among foragers have demographic analogues. Density-dependent mortality, like interference, can reduce the rate of local density increases. Depensatory mortality (Ricker, 1978) parallels Allee effects. However, care must be taken when interpreting the results of either behavioural or demographic computer simulations. These models are often based upon a stochastic environment which may or may not reflect natural resource variability. If the mechanism being simulated results in close tracking of resources, as appears likely in Hanski's (1980) simulations, then the observed b will be a direct result of the simulated environment's structure and randomness. The debate as to whether demography or behaviour is the chief cause of TPL (Anderson *et al.*, 1982; Hanski, 1980; Taylor *et al.*, 1983) will be difficult to resolve without detailed study of individual cases, where the result obtained may vary between studies. We believe that the fundamental phenomenon documented here is the ability of animal densities to match their resource distributions, and the mechanism responsible for this pattern will depend upon the spatial scale of the study relative to the mobility of the species being examined.

When TPL has a b of 2 due to environmental tracking, b will provide a poor index of spatial aggregation. The exponent of TPL will equal 2 for any constant value of α, including situations where all animals occur in one sample and where almost equal numbers of animals are found in each sample. Both a (representing the heterogeneity among samples if $b = 2$) and b (which may be affected by changes in α) must be considered when using TPL to quantify differences in aggregation among studies and species.

Conclusions

Consideration of the IFD does not conflict with previous demographic explanations for TPL (Hanski, 1980; Anderson *et al.*, 1982). The IFD makes predictions about TPL based upon mechanisms which operate within a population rather than those responsible for TPL among several spatially distinct populations. The mechanism of interest in a particular case will depend on the distances between samples and the mobility of the species involved. In contrast to Taylor's (1984: p. 334) assertion that "There is no theoretical justification in biology for knowing *a priori* how S^2 and $m[\bar{X}$ in this paper] are related..." the IFD can relate these parameters. We prefer the IFD and the behavioural models derived from it to the delta model (Taylor & Taylor, 1977) since they can be expressed in terms of observable behavioural processes and resource distributions, which can be studied independently of the TPL parameters and may lead to predictions of the TPL parameters in novel situations. The prominence of b values near 2 in both field studies and models suggest that environmental tracking is a major factor in determining the natural distributions of organisms. In this situation b provides a poor comparative measure of aggregation. In simulation models which produce close environmental tracking, caution should be employed in defining the patterns and variance of resource abundance, since these factors may be responsible for the TPL parameters generated.

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