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50 year anniversary of Lloyd's "Mean Crowding": ideas on patchy distributions.

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Abstract

1. This year marks the 50th anniversary of Monte B. Lloyd's "Mean Crowding" (1967) paper, in which he introduced a metric that accounts for an individual's experience of conspecific density.
2. Mean crowding allows ecologists to measure the degree of spatial aggregation of individuals in a manner relevant to intraspecific competition for resources.
3. We take the concept of mean crowding a step beyond its most common usage and illustrate that it has a mathematical relationship to many of the most important concepts in ecology and evolutionary biology.
4. Mean crowding, a first order approximation of the degree of non-randomness in a distribution, can function as a powerful heuristic that unifies concepts across disciplines in a more general way that Lloyd originally envisioned.

Keywords

Mean crowding; patchiness; spatial aggregation; experience of competition; selection; interdemographic selection; kin selection; host-parasite

Introduction

Monte B. Lloyd's "Mean Crowding" (1967) appeared 50 years ago in this journal and became a citation classic (> 250 citations) within 20 years of its publication (Lloyd 1986, Citation Classic 4, p. 13). Ecologists have used 'mean crowding' extensively, with 92.5% of all citations assigned by Web of Science to the research areas of Ecology, Entomology, Marine and Freshwater Biology, Zoology, and Agriculture. Furthermore, there is continued utility of the metric within ecology—as both a heuristic and an empirical tool—as evidenced

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Author Contributions

MJW conceived the ideas and carried out the algebra. MJW and CLF led the writing of the manuscript. CML contributed the mean crowding of parasites on hosts section. All authors contributed critically to the drafts and gave final approval for publication.

by the fact that Lloyd (1967) received an average of 24.22 citations per year over the 35 years between 1980 and 2015. Here, we review the ecological importance of mean crowding and discuss its expanded role in theoretical and applied evolutionary ecology. We show that the concept of mean crowding is fundamental for distinguishing random genetic drift from natural selection, and for characterizing kin selection, interdemic selection, and host-parasite co-evolution. We argue that this expansion of the conceptual domain of mean crowding stems from its simplicity as a measure of deviation from randomness, the ubiquitous null hypothesis for testing and detecting patterns in nature.

Lloyd's Mean Crowding

Prior to Lloyd (1967), ecologists interested in density-dependent processes relied primarily on measures of average density (see for example, Andrewartha & Birch 1954, Chapter 9, 'Other animals of the same kind'). Lloyd's central thesis, developed after discussions with C. S. Elton, was that dependence on measures of average density impedes attempts to understand the ecology and evolution of density dependent processes and density regulation because most animals tend to aggregate, i.e., group themselves into clusters. As a result of non-random spatial distribution, two individuals in the same population may experience vastly different levels of conspecific density. These differences in density might correspond to biologically important differences in competition, if resources are distributed randomly. Similarly, if individuals can exploit each other as resources or can manipulate each other in order to gain access to resources, higher levels of crowding might represent increased opportunity. Alternatively, if organisms follow an ideal free distribution, non-random differences in spatial distribution might not reflect differences in competitive regimes. Nonetheless, in that case, the patchy distribution of organisms might reveal something important about an underlying resource. In other words, even if the causes of aggregation remain obscure in any particular case, a statistic that measures the density that the average individual experiences is preferable to average density. As Lloyd (1986, Citation Classic 4, p. 13) expressed it, "...there is one thing about the habitat that can be measured and is undoubtedly important to the centipedes [of Wytham Woods], namely, the other centipedes in their immediate vicinity." Hence, Lloyd devised mean crowding as a measure of spatial patchiness that captured the biology of local density regulation from the perspective of the individual.

Mean crowding, m^* , measures density from the perspective of the individual. It is the average number of other individuals *per individual per unit of space* (typically, the quadrat). Lloyd's m^* differs from the average density as a function of the variance in density among local patches. We define m as the average density per quadrat ($m = \sum_i(n_i)/T$) and V_n as the variance in density among quadrats ($V_n = \{\sum_i (n_i)^2\}/T - (m^2)$). If n_i is the number of individuals in the i -th quadrat, each individual in that quadrat experiences the $(n_i - 1)$ other individuals in that same quadrat. Lloyd averaged across the population of individuals distributed across a total of T quadrats and obtained

$$m^* = \sum_i(n_i)(n_i - 1)/\sum_i(n_i) \quad (1a)$$

$$m^* = \left\{ \sum_i (n_i)^2 - \sum_i (n_i) \right\} / \sum_i (n_i) \quad (1b)$$

$$m^* = \left\{ \sum_i (n_i)^2 / \sum_i (n_i) \right\} - 1 \quad (1c)$$

We define m as the average density per quadrat ($m = E[n] = \sum_i (n_i)/T$) and V_n as the variance in density among quadrats ($V_n = \{ \sum_i (n_i)^2 / T \} - [m^2]$). We then substitute $(V_n + m^2)/(m)$ for $\{ \sum_i (n_i)^2 / \sum_i (n_i) \}$ in eq. (1c) to obtain

$$m^* = \left\{ V_n + m^2 \right\} / \left\{ m \right\} - 1 \quad (2a)$$

$$m^* = m + \left([V_n/m] - 1 \right) \quad (2b)$$

When individuals are distributed at random across quadrats, $(V_n/m) = 1$, and m^* equals m . When individuals are aggregated, as they might be around a shared resource, $(V_n/m) > 1$, and m^* exceeds m . Conversely, if individuals are over-dispersed, possibly as a mechanism to avoid competition, $(V_n/m) < 1$, and m exceeds m^* .

Because of its relationship to mean density under a random spatial distribution, Lloyd defined *patchiness*, P , as the ratio, (m^*/m) . Therefore, Lloyd's measure of patchiness is 1 when individuals are randomly dispersed among quadrats; greater than 1 if they are aggregated; and less than 1, when individuals are over-dispersed. Patchiness measures the *effective density* as experienced by the average individual. For example, if P equals 1.35 for some organism, then the individuals experience one another as though density were 35% greater than the average.

As a simple illustration, we use data on the distribution of the numbers of lice, *Brueelia tasniamae*, on their host rooks, *Corvus frugilegus* (Rozsa et al. 1996; Lang et al. 2017 Tables 3 and 4). Of 37 potential hosts inspected, 18 were infested with lice, totaling 787 individuals of *B. tasniamae*. The mean census of lice per infected bird was 43.7 but the mean crowding of lice per infected bird was 2.5 times higher, indicating that the louse numbers were aggregated on some hosts. Differently put, the average louse 'experienced' 109 other lice, a density 2.5 times higher than that suggested by the average sample size. As a second example, consider the experience of competition among graduate students within a lab for the potentially limited resource of Principle Investigator (PI) attention. Data from the Biological Sciences Division of a large Midwest university circa 1997 showed 278 graduate students distributed among 120 PIs (labs). This is an average density, m , of 2.32 graduate students per advisor. However, the distribution of these students among advisors was not random. The mean crowding, m^* , of graduate students around advisors was 3.87, indicating a strong tendency of the students to aggregate in or preferentially gravitate toward the labs of

some PIs but not others. The ratio of m^* to m , the *patchiness* of graduate students, was much greater than unity ($P_{graduate\ student} = m^*/m = 3.87/2.32 = 1.67$). Because students clustered, they experienced a more intense local competitive environment for attention from their advisors than suggested by the average density of graduate students. Because the clustering of students resulted in many under-populated labs, there was pressure from faculty to admit a greater number of graduate students. As a final example, Wade (1995, p. 121, eq. [12]) applied Lloyd's mean crowding to characterize selection on males in systems with resource-defense polygyny, wherein males guard patches of resource and mate with visiting females. He showed that, with a 1:1 sex ratio, the component of variance in male relative fitness owing to variance in relative mate numbers was equal to m^* , the mean crowding of females at resources (Wade 1995).

By and large, Lloyd's *mean crowding* has been used to address the fundamental problem of quantifying intraspecific competition. Indeed, of the 1,010 articles that have cited Lloyd (1967) to date, approximately 68% investigate the spatial distribution of one species or taxon, often calculating the average individual's experience of other conspecifics. In addition to this treatment of within species distributions, Lloyd (1967) developed an extension of his original metric in order to characterize interspecific crowding (the average subjective experience that each of two species has of the other) as well as a multi-species extension addressing the average individual's experience of biodiversity or species richness. Because Lloyd's subjective biodiversity metric is referenced by fewer than 10% of the citations to Lloyd (1967), we do not concentrate on it here. Instead, we focus on Lloyd's core concepts of mean crowding and patchiness as they apply to one and two species. Below we demonstrate formally that many of the important concepts in ecology and evolution have some version of mean crowding embedded in their key metrics.

Mean Crowding of Gametes Transmitted by Parents: the Distinction between Random Genetic Drift and Natural Selection

Distinguishing random genetic drift from natural selection often depends on determining *why* some parents contribute more offspring to the next generation than others. It is particularly problematic because offspring numbers often vary from one individual to another owing to random environmental influences.

The Wright-Fisher model is most often used to characterize random genetic drift, the effects of sampling of gametes on neutral gene frequencies in a finite population in the absence of selection. In this model of the fate of neutral alleles in a finite population, the number of offspring of one individual in a large population of size, N , is assumed to be Poisson distributed (Charlesworth 2009; Crow and Kimura 1970). A population of broadcast spawning, hermaphroditic marine organisms, with random fusion of gametes into zygotes, is a biological approximation to the idealized Wright-Fisher population model of genetic drift. A non-Poisson distribution of offspring numbers can arise by a number of processes, including natural selection, wherein some parents contribute more gametes than others than expected under a random distribution.

Because the biology of most natural populations deviates from the Wright-Fisher theoretical ideal population, Wright defined the ‘effective population size,’ N_e , as the size of the ideal population with the same rate of loss of heterozygosity per generation as a natural population of size, N . The strength of random genetic drift is inversely proportional to N_e and is important in several areas of evolutionary genetics, including inbreeding (Whitlock 1992, 2003; Frankham 1995), speciation (Carson 1968, 1975; Powell & Wistrand 1978; Templeton 1980; Carson & Templeton 1984; Bryant & Meffert 1988, 1990, 1996; Meffert & Bryant 1992; Meffert 1999), mating system evolution (McCauley & Taylor 1997), conservation biology (Hedrick & Kalinowski 2000), and Wright’s shifting balance theory (Wright 1931, 1978; Wade & Goodnight 1998; Goodnight & Wade 2000). Natural selection is one of the most important reasons that N_e is smaller than N because “a larger variance in offspring number than expected with purely random variation reduces N_e below N ,” (Charlesworth 2009, p. 196)

We illustrate the relationship between mean crowding and N_e by following Crow and Kimura (1970, p. 361–362, eq. 7.6.4.1). In a self-compatible, random mating diploid hermaphrodite population with a constant size, N , with discrete generations and no age structure, we let k_i be the number of gametes that the i -th parent contributes to the next generation, k be the mean number of gametes, and V_k the variance among parents in gamete numbers. The mean crowding of gametes around parents, m_k^* , is defined as $(k + [V_k/k] - 1)$. Hence, for this population, N_e equals

$$N_e = (k \cdot N - 1) / (k + [V_k/k] - 1) \quad (3a)$$

$$N_e = (k \cdot N - 1) / (m_k^*) \quad (3b)$$

When the distribution of gametes across parents is Poisson, then $k = V_k$, and $m_k^* = k$ in eqs. (3a and b).

With natural selection (other than balancing selection), however, the variance in offspring number (and hence gametes) among parents is greater than expected with purely random variation, so that $m_k^* > k$. This *reduces* the effective population size, N_e below N . Thus, the relationship between random genetic drift and natural selection is mediated by m_k^* .

We can go further with this relationship by recognizing that the variance in *relative fitness* is ‘the opportunity for selection’ (Crow 1958; Wade 1979, 1995; Shuster & Wade 2003). It is represented by the symbol, I , and is defined as the variance in individual relative fitness from all sources, environmental as well as genetic, within a population. It sets an upper limit on the amount of selective change that natural selection can cause in a generation. Expressed in terms of gamete numbers, the variance in individual relative fitness equals $V_k / (k)^2$. This allows us to rewrite m_k^* as $\{k(1 + I) - 1\}$, illustrating how the opportunity for selection changes the relationship between m_k^* and k with the result that the larger the value of I the greater the reduction in N_e . (With respect to one type of selection, sexual selection, Wade

(1995) showed that Lloyd's mean crowding of mates around males measures the component of the variance in relative male fitness caused by differences among males in mate numbers.)

Kin Selection: Mean Crowding among Altruists

In D. S. Wilson's theory of trait group selection (Wilson 1975), individuals of two types, A "donors" and B "recipients," in frequencies a and b , respectively, interact with one another in groups of size, N , during one stage of life. These interactions affect their own fitness as well as the fitnesses of other members in the group in the following ways: 1) A-types experience a fitness change, f_d , as a result of being donors and performing donor behaviors; and, 2) A-types and B-types experience a fitness change, f_r , as a result of being in proximity to donors. When there are several groups of size N , the frequencies of the two types in the i -th such group are a_i and b_i , so that N_{ai} is the number of A-type individuals in the i -th group and N_{bi} , the number of B-type individuals in the i -th group. Wilson (1975, p. 144, eq.[5]) gives this condition for the increase in frequency of A-types across the population as a whole, i.e., across all groups:

$$f_d > f_r \left\{ N \left(\left[\sum_i a_i b_i / \sum_i b_i \right] - \left[\sum_i a_i^2 / \sum_i a_i \right] \right) + 1 \right\}. \quad (4)$$

We multiply both terms in parentheses on the right hand side of eq. (4) by (N^2/N^2) to convert the frequencies, a_i and b_i , into numbers, N_{ai} and N_{bi} , of donors and non-donors, respectively, and obtain

$$f_d > f_r \left\{ N \left(\left[\sum_i (N_{ai})(N_{bi}) / N \sum_i N_{bi} \right] - \left[\sum_i (N_{ai})^2 / N \sum_i N_{ai} \right] \right) + 1 \right\} \quad (5a)$$

$$f_d > f_r \left\{ \left(\sum_i (N_{ai})(N_{bi}) / \sum_i N_{bi} \right) - \left(\left[\sum_i (N_{ai})^2 / \sum_i N_{ai} \right] - 1 \right) \right\}. \quad (5b)$$

We next substitute m_A^* for $(\left[\sum_i (N_{ai})^2 / \sum_i N_{ai} \right] - 1)$ and, Lloyd's measure of mean crowding between types (Lloyd 1967, p. 21, eq. [21]), m_{BA}^* , for $(\sum_i (N_{ai})(N_{bi}) / \sum_i N_{bi})$ and find

$$f_d > f_r \{ m_{BA}^* - m_A^* \} \quad (6a)$$

which can be rearranged to

$$f_d + (f_r) m_A^* > f_r m_{BA}^* \quad (6b)$$

Fitness changes to both A-types and B-types are the result of the behavior of A-types acting within groups. The net average fitness change for an A-type is the fitness change, $(f_d + f_r m_A^*)$, to an A individual *conditional on*, the average experience of other A individuals by a single A individual. Similarly, the net average fitness change for the B-type is the fitness

change, (f_i), to a B individual conditional on m_{BA}^* , the average experience of A individuals by a B individual. For the A-type to increase in frequency, the fitness change of an A-type must exceed that of a B-type; that is, A-types must be sufficiently aggregated (mean crowded) to offset the fitness cost, f_{cb} , of being a donor. Whenever a behavior by an individual (donor) of one genotype within a population affects the fitness of itself and other genotypes, the mean crowding of donors and the mean crowding of recipients (non-donors) by donors determine the distribution of the behavior's fitness effects.

Wright's Interdemic Selection: Mean Crowding of Migrants from Fitness Peaks

Wright (1932, 1977) proposed his Shifting Balance Theory (SBT) as a mechanism to select on gene combinations with epistatic effects on individual fitness. In his theory, demes at high fitness peaks exported their fitness-enhancing gene combinations to other demes in a metapopulation by selection between demes. Interdemic selection by the differential migration of individuals out from demes of high fitness and into demes of low fitness (rather than just random variation in migration) is one of the most controversial aspects of Wright's Shifting Balance Theory. It has since been shown in a laboratory interdemic selection experiment that, indeed, the strength of interdemic selection in Wright's SBT depended not only on variation in migrants exported across demes, but upon the mean crowding of those migrants. Using the experimental data from Wade (2013, p. 4, Table 1), we can see that, in the Control metapopulation (C_1), M , equaled 24.88 migrants per deme and the random variance about this mean was 24.92 (Wade 2013, p. Table 1, line 1). Thus, with entirely random migration, $M^* = M$. However, in the Experimental metapopulation (E_1), where *differential dispersion* as per Wright's Shifting Balance was imposed, M , equaled 24.86, nearly identical to the mean of the Control, but the variance in migration resulting from differential dispersion was more than 7-fold larger than random. As a result M^* was 31.24. (Wade & Goodnight 1991; Wade 2013). An intuition for this critical distinction can be strengthened by formulating interdemic selection in terms of mean crowding, which has been done by Wade (2013) and we reiterate here.

The interdemic selection differential, S , measures the degree to which migrants among demes in a metapopulation are a non-random sample from those demes. (The selection differential is often standardized [e.g., Falconer & Mackay 1996]). Let the number of migrants from the i -th deme equal M_i and define its mean as M , and its variance V_M . Wade (2013, p. 984, eq. [3b]) showed that the mean crowding of migrants around exporting demes, M^* , equals,

$$M^* = M + (V_M/M - 1) \quad (9)$$

The degree to which demes at high fitness peaks *differentially send out migrants* into demes at lower fitness peaks is the interdemic selection differential, that is, the difference, ($M^* - M$). Note that M^* equals M whenever the distribution of migrants is random (i.e., [V_M/M]

= 1). It is greater than M whenever $V_M > M$, that is, whenever there is directional interdemetic selection.

Host-parasite co-evolution: Mean Crowding of Parasites on Hosts

There is a tendency for parasites to be distributed unevenly among infected hosts, with most hosts having few or no parasites, while other hosts are highly infected (e.g., Wilson *et al.* 2001). Parasitologists use several measures to characterize this aggregation. The two most popular methods are the variance-to-mean ratio, V_m/m , and the dispersion parameter k in the negative binomial distribution (reviewed in Wilson *et al.* 2001). The mean crowding of parasites on hosts factors directly into both measures. The variance-to-mean ratio is contained within Lloyd's measure of mean crowding (eq. [1c]), but the ratio alone contains less information than m^* . Whereas mean crowding gives the average experience of parasite competition within hosts, the variance-to-mean ratio does not.

The dispersion parameter of the negative binomial distribution, k , is also related to mean crowding. As pointed out by Lloyd (1967, eq. [11]), under the assumption of a negative binomial distribution of parasites across hosts, the relationship between variance (V_m) and mean (m) is given by $V_m = m + (m^2/k)$. Substituting into eq. (2b) above, we find

$$m^* = m(1 + [1/k]). \quad (10)$$

This solution estimates k as the quantity, $m^2/(V_m - m)$, but it is only approximate (Wilson *et al.* 2002). Hence, Lloyds' original measure [eq. (2b)] is more straight-forward. Perhaps for this reason, more parasitologists have been using mean crowding to measure parasite aggregation (see calculations for aggregation indices in R at <http://www2.univet.hu/qpweb/>). It seems in general to be a more intuitive and direct measure of the competitive experience of parasites within or on hosts.

Summary

We have shown that Lloyd's formulation of mean crowding is intrinsic to some of the most important metrics and processes in ecology and evolutionary biology. By examining the relationship between mean crowding and measures of natural selection and random genetic drift, kin and interdemetic selection, and host-parasite co-evolution, We have demonstrated a feature that is common to all of these measures. That is, each of these fundamental concepts is concerned with a first order deviation from randomness. Indeed, if the distinction between randomness and pattern represents the central task of the ecologist and evolutionary biologist—to reveal the patterns in nature and to understand the processes that produce them—Lloyd's mean crowding, now 50 years old, is one of the most versatile tools available to biologists. Mean crowding is everywhere.

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