

Specificity of the spatial power-law exponent in ecology and agriculture

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Accounting for the spatial distribution of individuals is an important issue in ecology and applied biology. The exponent, b , in the established empirical relationship¹, $s^2 = am^b$, between s^2 , the spatial sample variance and m , the mean population density, conveys information about the spatial distribution of individuals of a particular species. When randomness occurs, variance and mean are equal. Usually $b > 1$ and, for given a , individuals randomly dispersed at some low density become more aggregated as density increases at a rate associated positively with the species' b value. The frequent recurrence of the same b value in field samples of a particular species has facilitated efficient sampling programmes² for pests and wildlife. But Downing³ claimed that the index b does not differ between species, is inconsistent within species, and is statistically biased, depending substantially and systematically on sample attributes. We report here technical deficiencies in his analyses and examine more substantial data that support none of these claims.

Our original collection⁴ of 156 data sets from the literature, later supplemented to 221 sets by Downing³, was not ideal⁵ for inter-specific comparison of b values, comprising samples of selected species collected by diverse methods at varying scales. Such data lack precision when units per sample $N < 15$ and sample pairs $M < 5$. With few high-density counts, they rarely yield the high variances that occur in systematic large-scale sampling studies. R , the range of values of $\log m$ in the regression form of the power law, $\log s^2 = \log a + b \log m$, should be as large as practicable. We therefore also analysed^{5,6} three data collections comprising all species adequately represented in large, standardized samples collected simultaneously, with tens of thousands of individuals from three major taxa over many years: 111 bird, 97 aphid and 263 moth species (Fig. 1).

Although values of b for a species may change with varying conditions⁷⁻¹¹, or vary with one factor such as scale or life-stage (for instance, ref. 53 in ref. 2) while remaining constant for others¹², there is mounting evidence for consistency of b when conditions vary little. Thus, analysis of parallelism in seven independent studies of *Aphis fabae*¹³⁻¹⁷ demonstrated² a common value of b ; and b did not differ between woodland and farmland environments in 103 of 111 bird species⁵. Values of b were consistent in independent studies in refs 20, 32, 41, 43, 44, 49, 58, 60, 83, 86, 93, 96, 97, 100, 110, 129, 147, 160 and 164, listed in ref. 2. Reports continually confirm negligible differences in b for pests in agricultural systems where environmental change is minor¹⁸⁻²⁰.

Although b incorporates a species-specific component, it is not a unique taxonomic character for separating species. Overall differences between b values within collections (Fig. 1) do not imply that every b value should differ significantly from every other, as Downing presumes³. Downing's analysis (his Fig. 1) is based on the statistically doubtful²¹ procedure of multiple pairwise tests and is questionable because the standard errors (s.e.s) of \hat{b} values are heterogeneous. Contrary to his conclusion that b values rarely differ, he found over 8,000 pairs of b values which differed significantly ($P < 0.1$), although less than 2,500 would be expected by chance if all species had the same b value.

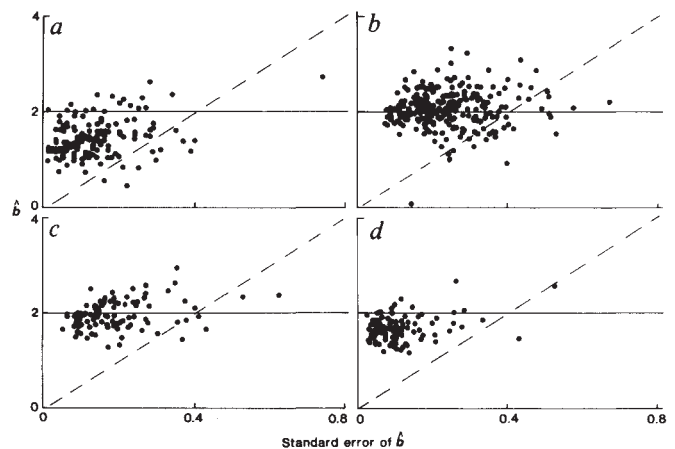


Fig. 1 Regression coefficients, \hat{b} , plotted against their standard errors for: a, 156 sets of data from the literature⁴; b, 263 moth species⁵; c, 97 aphid species⁵; d, 103 bird species⁵. Downing's criterion for data quality, s.e. $\hat{b}/\hat{b} < 0.2$ (dashed line), met by 78% of the regressions in his collection³, was achieved by 92%, 98%, 94% and 90% of regressions in a-d, respectively. Differences between b values are indicated when their variance is larger than that with which each is estimated; the ratio of between-to-within variance is, on average, 9.4, 4.1, 1.9 and 2.1 in a-d, respectively. If \hat{b} declined substantially³ with each of N , M and R , all of which are inversely related to s.e. \hat{b} , trends in plots of \hat{b} versus s.e. \hat{b} should be readily apparent, but are absent in a, b, c and d. Claims³ that values of $\hat{b} > 2$ (solid line) are rare for regressions with $N > 60$ or $M > 20$ or $R > 1$ are unsupported by data in b-d; by the above criterion of good data, hundreds of species have $\hat{b} > 2$.

Evidence³ that intra-specific b values differ is valid only when data are comparable and adequate. Of the 19 sets in Downing's Table 1, $N < 15$ in 11 sets and $M < 5$ in six; *Bosmina coregoni* compares horizontal variability in a eutrophic lake with vertical variability in a reservoir; *Leptinotarsa decemlineata* compares adults with eggs (\hat{b} is misquoted: 1.52 not 0.76); *Monodiamesa bathyphila* and *Limnodrilus hoffmeisteri* are extremely sparse data and one species determination is improbable²²; the *Popillia japonica* samples differ in scale; *Pieris rapae* compares caged with free-flying individuals, between continents where behaviour differs²³; *Pyrausta nubilalis* compares field plots with individual plants. Also, Downing's statement³ that \hat{b} is always lower where more samples are analysed is incorrect for four out of seven species. Also, the valid procedure²¹ is analysis of parallelism, not multiple t -tests performed on estimates of b with differing variances.

Downing's evidence³ of bias in \hat{b} (his Fig. 2) depends on his fitting regressions to sparse data sets ($N \leq 7$, $M \leq 5$ and $R < 0.5$) that ignore the heterogeneity of s.e.s of \hat{b} . No such clear trends are evident in our data nor is $\hat{b} > 2$ rare as Downing states³ (Fig. 1). Also, for each of four moth species⁵ with $\hat{b} > 2$: *Agrotis segetum*, *A. exclamationis*, *Lycophotia varia* and *Ellopiia fasciaria*, the M ranked yearly means were split into high and low sets, halving M and R ; analysis of parallelism shows b and $\log a$ are not affected ($F_{2,9} = 0.44$; $F_{2,9} = 0.08$; $F_{2,12} = 2.00$; $F_{2,12} = 0.77$, respectively, $P > 0.05$), demonstrating that bias is absent.

Barbour²⁴ reiterated^{1,2} difficulties with the estimator \hat{b} ; we had earlier discussed alternatives^{6,25,26}. Recent work¹¹ confirms that a variety of mechanisms may contribute to power-law data for a wide range of values of b , so Downing's arguments concerning models are no longer relevant.

This evidence confirms the efficiency of long-term programmes of repeated sampling based on the power law, now widely used to monitor crop pests^{2,27} and in wildlife conservation²⁸.

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Estimation of genetic trend in racing performance of thoroughbred horses

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Thoroughbred horses have been bred exclusively for racing in England since Tudor times and thoroughbred horse racing is now practised in over 40 countries and involves more than half-a-million horses worldwide. The genetic origins of the thoroughbred go back largely to horses imported from the Middle East and North Africa to England in the late seventeenth and early eighteenth centuries¹. Since the establishment of the Stud Book in 1791, the population has been effectively closed to outside sources, and over 80% of the thoroughbred population's gene pool derives from 31 known ancestors from this early period². Despite intense directional selection, especially on the male side, and the generally high heritabilities of various measures of racing performance³⁻⁵, winning times of classic races have not improved in recent decades⁶. One possible explanation for this is that additive genetic variance in performance may have been exhausted in the face of strong selection⁷. To test this, we have estimated the genetic trend in performance over the period 1952-77 using TIMEFORM handicap ratings which are based entirely on the horse's own performance, and express its racing merit as a weight in pounds which the compilers believe the horse should carry in an average free-handicap race. These ratings take into account such factors as the firmness of the ground, the distance and the level of the competition. Our results indicate that the failure of winning times to improve is not due to insufficient genetic variance in the thoroughbred population as a whole.

Our data consist of end-of-year ratings of three-year-olds, representing the best professional assessment of the merit of the horses based on their performances in that season. We have limited the study to three-year-old performances because many horses do not have a two-year-old performance rating, or retire from the track without receiving a four-year-old rating. We used a total of 31,263 three-year-old ratings representing the progeny of 2,087 stallions, for most of which a TIMEFORM rating was available. TIMEFORM ratings were also available for 59% of the dams. The means and standard deviations in TIMEFORM ratings for the sires, dams and progeny are given in Table 1.

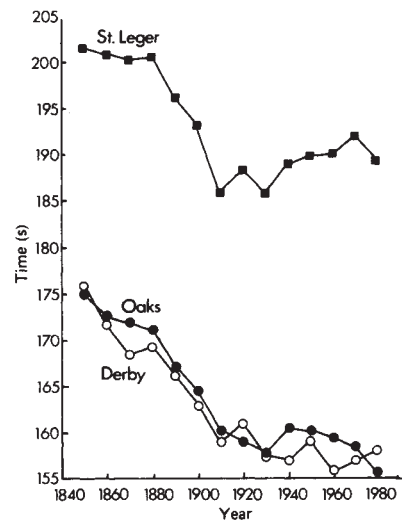


Fig. 1 Trends in winning times of the three principal classic races. Ten-year average winning times are plotted. The Oaks and Derby are 1.5-mile races for three-year-old fillies and colts respectively. The St Leger is a 1.75-mile race open to both sexes. Times were omitted for a few years when the races were run away from their usual venues. For years in which races were run over lengths different from the standard, winning times were adjusted for length of race and for change of pace associated with length.

Because there are consistent differences between the sexes, the progeny ratings are also given separately for colts, fillies and geldings. Because sires and dams are selected groups, their mean ratings are higher, and the standard deviations lower, than those of the progeny. The mean TIMEFORM ratings tend to decline over the period (regression of -0.32 ± 0.16 per year), reflecting the fact that more lowly rated horses have been included in the TIMEFORM ratings in recent years.

The distribution of progeny ratings is approximately normal (slight but significant skewness; non-significant kurtosis). If we assume normality, and also that the sires and dams are selected as an upper percentile from the progeny distribution, then it is possible to infer the selection intensity. Let the upper or selected percentile (p) begin at a value x on the abscissa, at which value the ordinate is z . The mean and standard deviation of the selected group are then $i = z/p$ and $\sigma_s = (1 - i(i - x))\sigma$. The means and standard deviations of the sire and dam ratings correspond to what would be expected if the sires represent the upper 6% of the distribution of colt ratings, and the dams the upper 52% of the filly distribution. These figures are also reasonably consistent with recruitment levels to the population as percentages of males and females born.

The average generation interval in thoroughbreds (defined as the age of the parents at the birth of their average offspring) has been estimated² as 10.1 years in the period since 1900. The average ages of sires and dams of a sample of 100 horses from the present study, born in 1981, were 11.2 ± 4.5 and 9.7 ± 3.8

Table 1 Means and standard deviations of three-year-old TIMEFORM ratings for 31,263 racehorses, for their 2,087 sires and for a proportion (59%) of their dams

| | Mean | s.d. |
|-------------|--------|-------|
| Sires | 126.63 | 7.70 |
| Dams | 91.34 | 15.78 |
| Progeny—All | 81.12 | 19.36 |
| —Colts | 88.89 | 18.98 |
| —Fillies | 78.17 | 18.21 |
| —Geldings | 72.53 | 13.73 |