

NULL MODELS AND THE "INTENSITY" OF SEXUAL SELECTION

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ABSTRACT: Null models can be used to determine the statistical significance of experimental estimations of the "intensity" of sexual selection (= variance in the number of matings/ square of the mean number of matings). Here, a null model is a stochastic arrangement of the data which maintains the mean number of matings but not the variance, permitting the statistical evaluation of the equality of variances with Levene's test. A bootstrap procedure is described for use with small data sets. Also, a relative measure of the "intensity" of sexual selection is defined (employing experimental and null values of selection "intensity") to facilitate comparisons between data sets derived from different populations, species, or experimental designs.

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A null model is a stochastic arrangement of data, with certain restrictions incorporated into the arrangement, which simulates the absence of some dynamic process. For instance, null models have proven useful in analyzing biogeographical data from which the presence of interspecific competition may be inferred after a comparison of the number of mutually exclusive species distributions in the real and null data sets (Conner, E. F. and D. Simberloff. 1984. Ch. 18, pp. 316-331. In: *Ecological Communities* [Strong, D. R., Jr. et al. eds.]. Princeton U. Press).

Here, I suggest that null models can be useful in determining the significance of the measured intensity of sexual selection. This is important since there is now concern that sexual selection is being invoked too readily as an explanation for observed patterns of behavioral interactions (Koenig, W. D. and S. S. Albano. 1986. *Am. Nat.* 127: 401-409). The intensity of sexual selection (or more accurately, the opportunity for sexual selection [see Crow, J. F. 1958. *Hum. Biol.* 30: 1-13]), I_s , is defined as the variance in the number of matings divided by the square of the mean number of matings (Arnold, S. J. and M. J. Wade. 1984. *Evolution* 38: 709-719; Wade, M. J. and S. J. Arnold. 1980. *Anim. Behav.* 28: 446-461). Thus, where a few individuals obtain most of the matings I_s is large, while I_s is small in populations where mating success varies little among individuals. It is important to note that even under random mating the value of I_s may not be zero. The estimation of I_s through mark-recapture studies permits an evaluation of the potential for sexual selection to effect phenotypic change.

A data set from which I_s is calculated contains two types of information: 1) the number of times each individual was sighted, and 2) the number of times each individual was observed mating. A null simulation of the data set can be generated as follows. First, keeping the number of observations per individual the same as in the original data set, assign matings to individuals at random with the restriction that no individual receives more matings than the number of times that individual was sighted. Then, assign matings at random until the total number of matings in the simulation equals the number of matings in the data set. Therefore, the mean number of matings will be equal between the null simulation and the original data set, but their variances may differ. Differences in variance can be tested with Levene's test (Van Valen, L. 1978. *Evol. Theory* 4: 33-43;

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Schultz, B. B. 1985. Syst. Zool. 34: 449-456).

In Levene's test, each variate is converted to an absolute deviation (= new variable) from the estimate of central location (mean or median). The means of the new variable can then be compared via a t-test or an analysis of variance. In general, the use of the median proves more robust than the use of the mean for converting the original variates to new variables (Schultz, B. B. 1983. Evol. Theory 6: 197-203). The median-Levene's test is more powerful than other robust tests (Schultz, B. B. 1985. Syst. Zool. 34: 449-456).

Simulations and data analysis.

I have generated three null models for each of four data sets and for illustrative purposes have only tested the largest null value for I_S (= I_{Sn}) against the appropriate data set value with median-Levene's test (Table 1). It is evident that there is variation in the null values derived from a single data set and that, depending on characteristics of the data set, null values can be quite large. One of the estimations of I_S from the data sets is seen not to be significantly larger than I_{Sn} , the null value. Simulations reveal that relative variation in I_{Sn} is less the larger the data set. Therefore, for large data sets the statistical significance of an observed I_S could be reasonably tested with a single null simulation via Levene's test. However, for small data sets, which may give rise to more variable values of I_{Sn} , statistical significance should not be tested in this manner. Instead, an empirical distribution of I_{Sn} values should be constructed from numerous null simulations. Next, it would be necessary to determine if I_S lies within the 95% confidence interval around the mean of I_{Sn} .

Table 1. Observed (I_S) and null (I_{Sn}) values of the intensity of sexual selection for four insect data sets. t = test statistic for Levene's test ($P < 0.05$ is indicated by an asterisk) for comparisons between I_S and I_{Sn} . I_{Smax} = maximum possible value for I_S (see text). $I_{Sr} = (I_S - I_{Sn}) / (I_{Smax} - I_{Sn})$. n is the number of individual males observed.

Species	I_{Sn}	I_S	I_{Smax}	I_{Sr}	n	t
<i>Neacoryphus bicrucis</i> ^a (Hemiptera: Lygaeidae)	0.37-0.48	0.94	4.20	0.12	60	2.59*
<i>N. bicrucis</i> ^b	0.10-0.20	0.29	1.43	0.07	40	0.88
<i>Tetraopes tetraophthalmus</i> ^c (Coleoptera: Cerambycidae)	0.27-0.35	0.55	1.35	0.20	45	1.78*
<i>T. tetraophthalmus</i> ^d	0.99-1.10	2.82	8.81	0.22	281	15.27*

^a Males occupying small defendable mating territories of variable quality (see McLain, D. K. 1986. Oikos [in press]). All males observed 14 times.

^b Males in large, high quality, but undefendable territories. All males observed 14 times.

^c Males observed four times (see McLain, D. K. and R. D. Boromisa. 1987. Behav. Ecol. Sociobiol. [in press]).

^d Males observed 1-12 times.

Two data sets for the milkweed beetle, *Tetraopes tetraophthalmus*, are from the same population. Yet, the value of I_S differs greatly between them. One data set is a subset of the other: in one case only males sighted four times are included, to eliminate potential effects of natural selection (e.g. on viability, since longevity may correlate with the number of matings), and in the other case

all individuals are included (representing males sighted 1-12 times). Thus, the measured intensity of sexual selection can vary greatly depending upon how the data are calculated (or how the experiment is conducted).

Therefore, I would like to suggest that null values be reported along with field estimates of I_s to facilitate the evaluation of the magnitude of I_s . In fact, it may be more instructive to report I_s along with a measure of its proportion of the total possible intensity of sexual selection. This proportion, I_{sr} ("r" for relative), will be determined in part by the total number of matings observed and the distribution of the number of sightings per individual. I_{sr} will have a maximum value of 1.0 and can be calculated as $(I_s - I_{sn}) / (I_{smax} - I_{sn})$. Here, I_{smax} is the maximum possible value of I_s and is calculated by allocating the most matings possible (= number of observations) to individuals until the number of matings allocated equals the number observed, then assigning 0 matings to the remaining individuals, and finally calculating the variance/ square of the mean number of matings. Thus, I_{sr} represents the proportion of the total possible intensity (opportunity) which was realized, correcting for the fact that the null value of I_s (= I_{sn}) not $I_s = 0$ represents the minimum or reference value. For small data sets the mean of a number of I_{sn} should be used to calculate I_{sr} .

The theoretical minimum value of I_{sr} will be 0 except under a monogamous mating system. The measure of I_{sr} in a monogamously mating population will be less than 0 since monogamy results in a less variable distribution of matings than does mating at random. Thus, the measured I_s will be less than I_{sn} . Monogamy, then, is a deviation from random mating which is in the opposite direction as the deviation of polygyny from random mating. Monogamy will be unambiguously detectable in practice if females are also individually marked.

The values of I_{sr} and I_{smax} are presented in Table 1. Now, it can be appreciated that the large value of I_s for all milkweed beetles is no greater proportion of the theoretical maximum than is the value of I_s determined for the subset of individuals sighted only four times. Of course, the apparent precise congruence between I_{sr} for these two data sets is coincidental (fractionation of other data sets proves this).

In conclusion, null models represent a useful device for determining the significance of experimentally determined I_s 's and for estimating the relative magnitude of I_s . The value of I_{sr} should be useful for comparing the strength of the intensity of sexual selection between different populations or species.

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