



The Effect of Relative Frequency of Species in Competition: A Reappraisal

P. D. Putwain; J. Antonovics; D. Machin

Evolution, Vol. 21, No. 3 (Sep., 1967), 638-641.

Stable URL:

<http://links.jstor.org/sici?sici=0014-3820%28196709%2921%3A3%3C638%3ATEORFO%3E2.0.CO%3B2-M>

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

Evolution is published by Society for the Study of Evolution. Please contact the publisher for further permissions regarding the use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/ssevol.html>.

Evolution

©1967 Society for the Study of Evolution

JSTOR and the JSTOR logo are trademarks of JSTOR, and are Registered in the U.S. Patent and Trademark Office. For more information on JSTOR contact jstor-info@umich.edu.

©2003 JSTOR

NOTES AND COMMENTS

THE EFFECT OF RELATIVE FREQUENCY OF SPECIES IN COMPETITION: A REAPPRAISAL

P. D. PUTWAIN, J. ANTONOVICS, AND D. MACHIN

Department of Agricultural Botany, University College of North Wales, Bangor.

Received January 20, 1966

In his paper "The effect of relative frequency of species in competition," (Evolution, 19, 350-4, 1965), Takashi Narise has derived the following conclusions from his data. First, that the outcome of a struggle between *Drosophila melanogaster* and *D. simulans* depended on their relative frequency in the parental generation. Second, that the relative output of *D. simulans* was enhanced at the lowest density, (10 pairs), although output of *D. melanogaster* was relatively better overall. From these results he claimed to show

"how a weaker competitor indigenous to an area can prevent a strong competitor from colonizing this area, if migrants are so low in number that the frequency of the indigenous species is always high."

It is considered that the interpretations he put on his results are misleading.

De Wit (1960) in examining the interactions between two species occupying the same "space" has envisaged exactly the same situation where outcome of a struggle between two species is fre-

quency dependent. In an elegant model de Wit plots the log of the output ratio (Species 1/Species 2) against the log of the input ratio (Species 1/Species 2). The advantage of such a ratio diagram over a frequency diagram is that if the relative effect of a group of organisms upon another group is the same over the whole range of input frequencies, then the ratio diagram will maintain unit slope over the range of input frequencies. This is far easier to interpret than the curve produced by a frequency diagram. Furthermore, if the relative advantage of one group over another is frequency dependent this is easily noted as a departure from unit slope.

If the situation envisaged by Narise was true, that is, a species with a low relative frequency was at a greater disadvantage than at a higher relative frequency, the resulting diagram should be similar to Figure 1a, that is, the graph should cut across the unit slope line at some point along the input ratio axis. The average number of emerged flies per bottle in *cn* : *bw* and *D. simulans* was replotted in the form of a ratio diagram

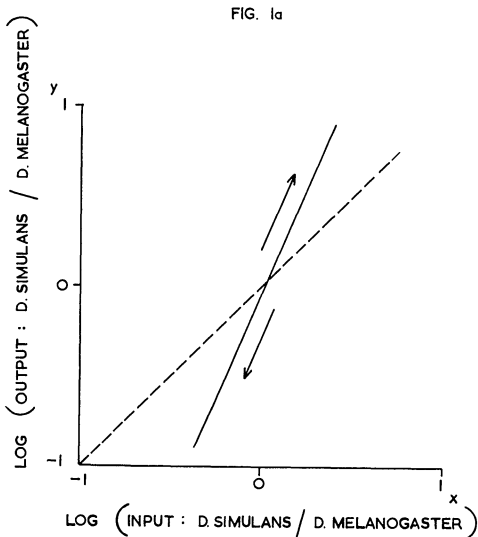


FIG. 1a. Theoretical ratio diagram of a situation where the minority component of a mixture is at a disadvantage.

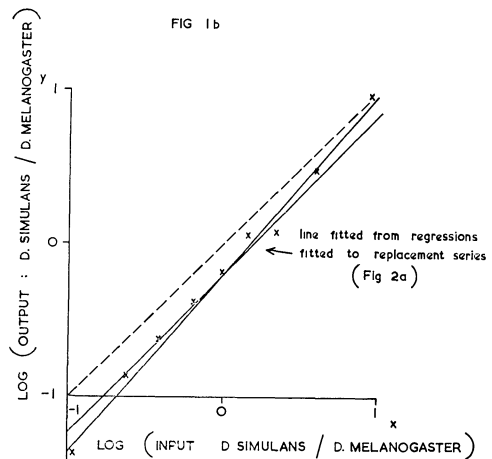


FIG. 1b. Ratio diagram of interactions at low density (10 pairs). Regression $y = -0.21 + 1.17x$, significant at $P < .001$.

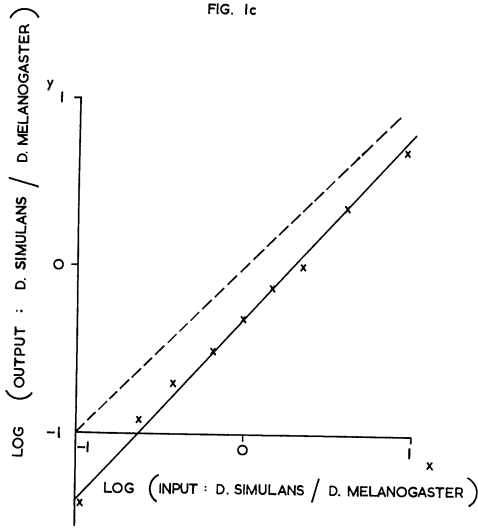


FIG. 1c. Ratio diagram of interactions at medium density (20 pairs). Regression $y = -0.32 + 1.11x$, significant at $P < .001$.

(Fig. 1b). It is seen that this does not conform to the pattern of Fig. 1a. The low density data do not provide any real evidence that *D. melanogaster* would lose in a struggle with *D. simulans*. The ratio diagram graph calculated from the real data suggests that it *might* be possible for *D. simulans* to win if the relative input ratio of *D. simulans*/*D. melanogaster* became greater than 9 : 1. Since only 10 pairs of flies were used at

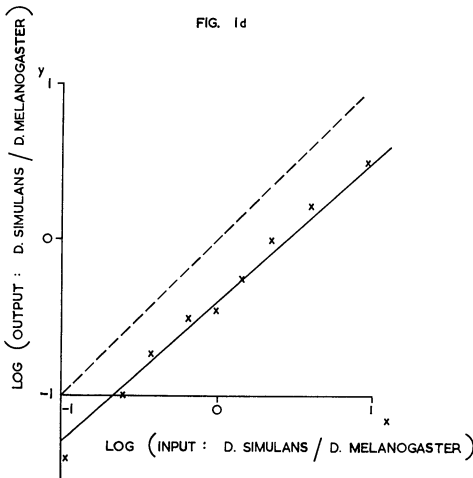


FIG. 1d. Ratio diagram of interactions at high density (30 pairs). Regression $y = -0.35 + 0.50x$ significant at $P < .05$.

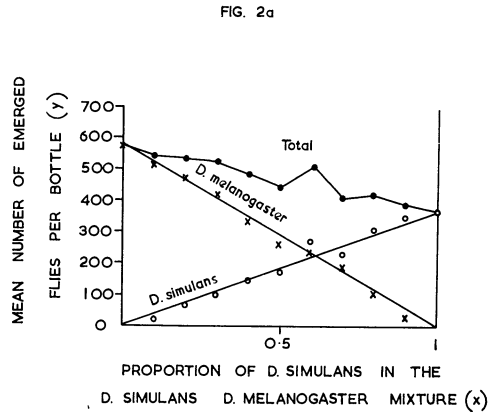


FIG. 2a. Replacement series graphs of interactions at low density (10 pairs). Regression equations:

D. melanogaster $y = 575x$ significant at $P < .001$.
D. simulans $y = 375x$ significant at $P < .001$.

this density level, then, under the conditions of this experiment, a higher ratio is clearly impossible. An increase in overall density in order to make higher ratios of *D. simulans*/*D. melanogaster* possible, would progressively lead to the situation where *D. simulans* is always the loser whatever the input ratio. This can be seen from the high density data (Fig. 1b). This was taken a step further and the data were plotted as "replacement series graphs" as in Figs. 2a, b, and c. It is seen that the medium and high density data

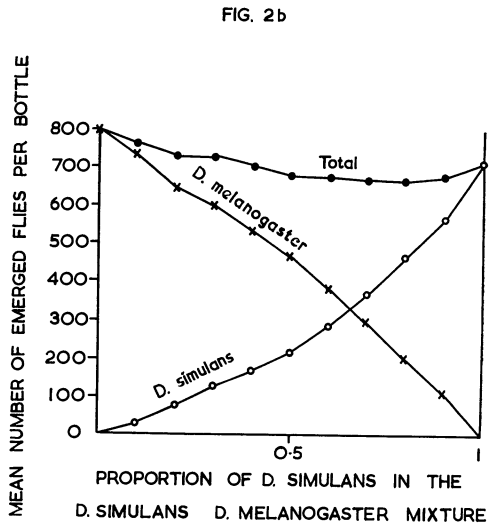


FIG. 2b. Replacement series graphs of interactions at medium density (20 pairs).

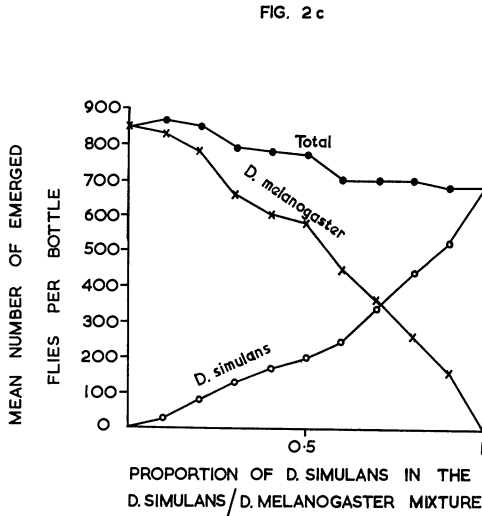


FIG. 2c. Replacement series graphs of interactions at high density (30 pairs).

fit the situation described by de Wit where two species crowd for the same space. But at low density there appears to be no interference between the species. Linear regression lines were fitted to the low density data, conditional on passing through the origin (Fig. 2a) and the ratio values which were calculated from the regression lines were then plotted on the ratio diagram (Fig. 2b). The ratio line so obtained is parallel to the unit slope line and its slope (1.17) is not significantly different from this line. Evidence from ratio diagrams and replacement series graphs suggests that Narise's main conclusions may be erroneous.

It is a curious feature of the experiment that the density dependent effect on selection pressure claimed by Narise was acting in an unexpected direction. For it was only at the lowest density, where the environment was apparently non-limiting, and interference from the other species at a minimum, that there was strong sign of a frequency dependent effect. Measurements of mating success (the percentage fertile females) at different frequencies and densities showed interesting effects but they were not clearly in the direction of an increased frequency effect at lower densities. It is very difficult to envisage a natural situation where an aggressor A fails to colonize an area occupied by a species B only at low density levels.

There is a further point which explains Narise's assertion that the outcome of a struggle between *D. simulans* and *D. melanogaster* depended on the initial relative frequency of the two species. He may have seriously overestimated k , the com-

petitive value, at lower densities and lower frequencies of *D. melanogaster*. Narise defines

$$k = \frac{p}{q} \frac{r}{1-r}, \text{ where } q = (1-p) \text{ is the relative frequency of } D. \textit{simulans} \text{ parents and } r = \text{the relative frequency of } D. \textit{simulans} \text{ progeny.}$$

He calculates the estimator of k as

$$k' = \frac{1}{m} \sum k_i = \frac{p}{q} \frac{1}{m} \sum \left(\frac{r_i}{1-r_i} \right) \quad (1)$$

where $i = 1, 2, \dots, m$ is the number of replicates.

We can calculate by standard procedures the expected mean and variance of k' assuming that r_i is distributed as a binomial with mean θ and variance $\frac{\theta\phi}{n_i}$ where $\phi = 1 - \theta$ and n_i is the number of observations in the i^{th} replicate.

$$Ek' \sim \frac{p\theta}{q\phi} \left\{ 1 + \frac{1}{m} \sum \frac{1}{n_i\phi} + \dots \right\} \quad (2)$$

$$\text{Var } k' \sim \left(\frac{p\theta}{q\phi} \right)^2 \left\{ \frac{1}{m^2} \sum \frac{1}{n_i\theta\phi} + \dots \right\} \quad (3)$$

We see that k' overestimates k^* , the bias and the variance increasing with increasing θ . We can thus expect larger positive deviations from the regression line of k' against q as θ increases, and a transformation of the k_i would seem to be necessary before analysis of variance is attempted, the bias may not be serious in Narise's calculations as $n_i \geq 300$.

An alternative $k'' = \left(\frac{p}{q} \frac{\bar{r}}{1-\bar{r}} \right)$, more suitable

for situations where small numbers are unavoidable, can be shown to be an almost unbiased estimator of k with variance equal to $(\text{Var } k')/m$.

As density (the number of pairs) is decreased, random effects would be expected to increase. Thus, the greater rise in the value of k at the lowest density level (10 pairs) could again be spurious. The argument suggesting *D. simulans* reproduced relatively better when it was at a high relative frequency revolved around the fact that the average k value calculated for the low density level at *D. simulans* input frequency of 0.9 was 1.4627. This may be because when *D. melanogaster* is at the relative frequency of 0.1 as well as at the lowest density level (i.e., 1 pair), stochastic processes are likely to be most serious (Lerner and Dempster, 1962), and tend to inflate his estimates of k most. Seen in the de Wit form, the relative performance of *D. simulans* at the

(*) The proof that k' is a biased estimator of k does not depend on the binomial distribution for r_i .

lowest frequency in the lowest density does not appear to be beyond the normal error variation.

Thus, it is suggested that the interrelationships between *D. simulans* and *D. melanogaster* can be more correctly interpreted and presented by the use of de Wit's ratio diagrams and replacement series graphs.

Acknowledgments.—We would like to thank Professor J. L. Harper and Dr. A. D. Bradshaw

for their useful comments and critical reading of the manuscript.

LITERATURE CITED

- LENER, I. M., AND E. R. DEMPSTER. 1962. Indeterminism in interspecific competition. *Proc. Nat. Acad. Sci.* **48**: 821–6.
 WIT, C. T. DE. 1960. On competition. *Versl. Landbouwk. Onderz.* **66**: 8–82.

THE LOSS OF THE OPHIDIAN MIDDLE EAR

D. S. BERMAN AND P. J. REGAL

Zoology Department, University of California, Los Angeles

Received July 26, 1966

The absence of the tympanic membrane, tympanic cavity, and Eustachian tube in snakes is usually explained as the result of degeneration due to the reduction of air-borne stimuli in the ancestral environment of the hypothetical burrowing antecedents of snakes. Evidence for this theory is usually based on a correlation between middle ear reduction and burrowing habits in lizards, as is noted by Bellairs and Underwood (1951). Similar lines of reasoning are followed by other authors. But this sort of evidence, based on analogy, gives no real proof that the degeneracy of the middle ear of snakes was in response to burrowing.

Loss of the tympanic system in lizards cannot always be correlated with burrowing habits. Smith (1938) points to regressive changes in the middle ears of lizards leading an active life both on the ground and in the trees. These changes span the gap from the typical lizard condition to one comparable to that seen in snakes, (e.g., arboreal Chamaeleons) and yet it is not obvious that their sound environment is lacking and it seems probable that they would benefit by having good hearing powers. This suggests that diapsid reptiles must have lost the tympanic system for a variety of reasons.

A functional relationship between burrowing and a reduction of the tympanic system has been suggested for the sand-dwelling horned lizard, *Phrynosoma m'calli*. Forward displacement of the depressor mandibulae by the enlargement of the cervicomandibularis muscle has completely occluded the ear opening, resulting in a degeneration of the tympanum and the reduction and attachment of the extra-columella to the quadrate bone (Norris and Lowe, 1951). The enlargement of the cervicomandibularis muscle is attributed by the authors to its function in the burrowing movements of the head. This situation does not apply in modern snakes.

Tumarkin (1949, 1955) advances a contrary notion that articulation between stapes and quadrate is primary and that the typical lizard condition, or "vestibulo-tympanic" condition, is secondary. Tumarkin's assertion is that there has been a retention in snakes and some lizards of the primitive condition, whereas most lizards display an advanced sound conducting system which has evolved independently in several lines of tetrapods. Regardless of the validity of either line of reasoning, we are still confronted with the question of what factors might have prevented present day terrestrial or arboreal snakes from evolving a typical middle ear structure capable of monitoring air-borne vibrations. Wever and Vernon (1960) have demonstrated that though the ophidian ear is limited in its frequency response, snakes are not deaf to aerial sounds.

Current theories accounting for the absence of the ophidian middle ear depend on hypothetical circumstances in the early evolution of snakes and argue by analogy to lizards with only a vague reference to the actual selective or nonselective factors hypothetically involved. We feel that there is an alternative explanation to the line of reasoning which argues loss through non-use. This is based on conditions common to the vast majority of living snakes and is related to the highly specialized ophidian feeding mechanism.

The ophidian feeding mechanism is distinctive and complex. Both the upper and lower jaws on either side of the head move independently and alternately and the associated bones are but loosely articulated. The series of loose linkages suspending the lower jaw may be visualized as somewhat like that represented by the human arms with the hands unclasped. The loose joints at the elbow and shoulder correspond roughly to the mandibular-quadrate and suspensorium-supratemporal articulations respectively. The unclasped hands represent the liberation of the man-