On the Measurement of Total and Sexual Selection: A Reply to Christiansen

Gonzalo Alvarez, Mauro Santos, Carlos Zapata


Stable URL:
http://links.jstor.org/sici?sici=0014-3820%28198405%2938%3A3%7C2%7COTMOTA%3E2.0.CO%3B2-8

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*
©1984 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.

©2002 JSTOR

http://www.jstor.org/
Thu Sep 26 03:13:09 2002
ON THE MEASUREMENT OF TOTAL AND SEXUAL SELECTION: A REPLY TO CHRISTIANSEN

GONZALO ALVAREZ, MAURO SANTOS, AND CARLOS ZAPATA
Departamento de Genética, Facultad de Biología, Universidad de Santiago de Compostela, Santiago de Compostela, Spain

Received July 15, 1983

Alvarez et al. (1984) have demonstrated that the frequency-dependent fitnesses, for both total and sexual selection, reported by Bundgaard and Christiansen (1972)—hereafter quoted as B&C—are spurious due to an erroneous procedure for fitness estimation, and that the balancing mechanism responsible for the maintenance of the chromosome polymorphism of Drosophila melanogaster studied by B&C is not frequency-dependent selection favoring the rare genotype but heterosis with practically constant fitness values. In our paper we proved that total fitness estimates from B&C, which are obtained as the product of the estimates of partial fitness components, are exactly the same as those that arise by means of the Polivanov (1964) estimators and, moreover, that the partial fitness estimators from B&C for sexual and fecundity selection also produce spurious results.

Christiansen (1984) has claimed that our paper is a reiteration and that in the B&C work “the analysis of data was used to emphasize the structure of the commonly used total fitness estimators (Polivanov, 1964), which are heavily biased as shown by Prout.” However, although the frequency-dependent fitness pattern found by B&C for both total and sexual selection is repeatedly quoted by Christiansen (1984) as an apparent one, the term apparent, or similar ones (spurious, erroneous, etc.), is never used by B&C to characterize the frequency-dependent pattern observed. Moreover, the only comment on the properties of the total fitness estimators in the B&C work is that “the bias of the estimators of \( W_u \) [total fitness] and \( \Delta p \) has been studied and was found to be negligible in this study.” Evidently, B&C are referring to the statistical bias and nothing is said about the spurious frequency-dependent selection generated by the existence of post-observational selection. Therefore, it seems to us that Christiansen (1984) is doing an “a posteriori” interpretation of the B&C work.

On the other hand, with regard to the methods for estimating partial fitness components, Christiansen (1984) argues that “Alvarez et al. (1984) state that the basic error in using for sexual selection estimators of the form of the total fitness estimators of Polivanov (1964) is that sexual selection and the mating pattern are confounded. However, this is not the basic error of those estimators. Even for random mating spectacular biases will occur, as they are caused by including segregation and zygote for-

mation into the sexual selection component (Prout, 1965; Christiansen et al., 1977).” Clearly, Christiansen turns around our arguments and, moreover, he overlooks some aspects on fitness estimation. We have never confirmed that the sexual estimator confounds sexual selection and pattern of mating, but these two phenomena are confounded by B&C. Thus, on page 447, to derive the formulas for the sexual fitness estimators, B&C state: “The sexual fitness values . . . are those created by deviations in the adult mating pattern from the one expected had the unmated adult population mated at random.” It is obvious that B&C do not properly differentiate sexual selection, which involves frequency of mating, and pattern of mating, which is not a selective agent and concerns choice of mate. This misunderstanding of the operation of selection at the level of mating behavior is really the origin for constructing an inappropriate sexual estimator. As a consequence of this erroneous definition of sexual selection, the sexual fitness estimator is comparing two sets of genotype frequencies which are not implicated in the action of sexual selection, and so it produces erroneous fitness estimates. Therefore, the claim made by Christiansen that the problems discussed by Prout (1965) and Christiansen et al. (1977), which deal with the estimation of total selection, are the causes of the incorrect estimation of sexual selection, does not make sense.

In the “structural analysis of the mating pattern” from the B&C article they develop three kinds of sexual fitness estimators in order to analyze the components of mating behavior: female and male mating success \( W_f \) and \( W_m \), respectively) and joint mating success \( W_{n,0} \). We have shown that whereas \( W_f \) and \( W_m \) correctly estimate female and male sexual selection, \( W_{n,0} \) produces spurious frequency-dependent fitness estimates, and that non-significant deviations of random mating are occurring in their experimental populations (Alvarez et al., 1984). Nothing of this is indicated in the B&C work. Thus it seems to us that Christiansen (1984) reinterprets the B&C article again when he affirms that in the structural analysis of the mating pattern they do separate sexual selection from the combination rules in mating.

LITERATURE CITED
Alvarez, G., M. Santos, and C. Zapata. 1984. Frequency-dependent selection arising from in-


Corresponding Editors: J. Felsenstein, D. Futuyma

---

**THE SOCIETY FOR THE STUDY OF EVOLUTION**

**APPLICATION FOR MEMBERSHIP**

(You may photocopy this form)

Name ___________________________________________ Dr. Miss Mr. Ms. Mrs. Prof. (circle one)

Last

First

Middle

Department ___________________________________________

Institution ___________________________________________

Mailing address for EVOLUTION and for Society communications:

________________________________________________________________________

________________________________________________________________________

________________________________________________________________________

________________________________________________________________________

Zip Code __________________________

**CLASS OF MEMBERSHIP DESIRED AND ANNUAL DUES**

_____ Student Members $20.00. Signature of Faculty Member ________________

_____ Members $35.00

_____ Each additional family member add $1.00

_____ Sustaining Member $70.00

_____ Life Member $700.00

(20 times annual dues)

_____ Subscribers $60.00

_____ Non-U.S. members and subscribers should add $5.00 for mailing charges.

(All classes of membership include one subscription to EVOLUTION.)

Send completed application with check to:

Dr. Robert Beer, Treasurer
Department of Entomology
University of Kansas
Lawrence, Kansas 66045 USA