### **Accepted Manuscript**

What is adaptation and how should it be measured?

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PII: S0022-5193(18)30110-3 DOI: 10.1016/j.jtbi.2018.03.003

Reference: YJTBI 9380

To appear in: Journal of Theoretical Biology

Received date: 17 May 2017
Revised date: 27 February 2018
Accepted date: 4 March 2018



Please cite this article as: Joel R. Peck, David Waxman, What is adaptation and how should it be measured?, *Journal of Theoretical Biology* (2018), doi: 10.1016/j.jtbi.2018.03.003

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#### ACCEPTED MANUSCRIPT

## Highlights:

- A quantitative measure of adaptation is proposed.
- Changes in parameter values can alter mean adaptation and mean relative fitness in opposite directions.
- Applications to the units of selection and the major transitions in evolution are considered.



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