# Waddington's Revision Of Haldane

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- *From*: "John W Edser" <edser@xxxxxxxxxx>
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I have repeatedly objected to Waddington's revision of Haldane's basic
population genetics equations being ignored within gene centric Neo
Darwinism. Jim
Menegay expressed interest in Waddington's revision and asked the
professionals that
post here for clarification. None has been forth coming. Therefore I have
decided to post
some of the photostate that I have. The cover sheet was lost so I cannot
give the exact
reference. As I recall they were copied from Waddington's book "The
Evolution Of An
Evolutionist". Perhaps somebody else can supply the exact refrence. Here are
what I
consider to be the appropriate parts which I will post without comment.

−−−−−−−−−−−−− Beginning of Waddington's Revision of Haldane−−−−−−−−−−−−−−−−

THE NECESSITY TO CONSIDER MORE THAN ONE ENVIRONMENT
The strict Neo−Darwjnist paradigm is unsatisfactory in another respect,
namely,
that it involves only one uniform environment, through which natural
selection is
exerted in a form which requires specification by one single coefficient for
each
type of biological entity. Again, as with the omission of the phenotype,
there are
several different objections to this − though, perhaps they should be
regarded as
different aspects of a basic general objection.

To put the matter abstractly first: there arc only two sources of
evolutionary
change; alterations in the environment, or alterations in genes. A paradigm
in terms
of a single uniform environment implies either attainment of an equilibrium,
or
evolutionary changes brought about by the appearance of new genes. But the
latter
is a very weak prop to rely on, since it is normally held that all possible

mutations
are constantly occurring at definite frequencies. One could perhaps escape
this
dilemma by appealing to rare mutational events involving large scale
restructuring
of the geno-type (additions, deletions, inversions, etc.), or rare
incorporation of
large masses of genetic information by processes such as introgressive
hybridization,
incorporation of episomes etc, but this would be an uncomfortable basis for
a general
theory of evolution.
..
On a more pragmatic level, one may ask whether the concept of a single
uniform
environment is ever even conceivably applicable in the real world, which
appears
inescapably heterogeneous. And if it is not, it should be remembered that
evolution
provides mechanisms by which any initial inhomogeneity will become either
exaggerated
in kind or increased in the number of sub−regimes. For instance, if we start
with a
total universe containing two environmental regimes (niches) A and B, each
dominated
by a biological species A' or B', that it will always be possible for some
evolutionary
descendant of one or other of these species to delimit as its own niche some
appropriate function of the previously existing entities F(A,B,A'B'); indeed
there is
an infinite set of such functions to be used in this way. This is the
general explanation
for one of the features of evolution which seems to prove most puzzeling to
physical sceintists, who ask why such an enourmous variety of different
types
should have been produced, althought the existence of primatve organisms
such
as bacteria, at the present day, proves that they are functionally quite
'fit' enough
to surive.
[..]
Suppose there are two clones A and a, and two environments X and Y,
with frequencies p and l−p. As case 1 let us assume that a
proportion q of organisms is selected in X and 1−q in Y. Then for
each clone we have:

Developed in X Developed in X Developed in Y Developed in Y
Selected in X Selected in Y Selected in X Selected in Y
pq p(1−q} q(l−p)
(l−p)(1−q)

Suppose clone a has perfect adaptiveness, i.e. always has full natural selective efficiency in the environment in which it developed. Then its coefficients would be :

1 1−k1 l−k2
1

But let clone a be fully canalized for X, i.e. show full natural selective efficiency in X whatever environment it had developed in. Its coefficients would be:

1 1−k3 1
1−k4

Simplifying further, we may assume that the chance of being selected within an environment is proportional to the frequency of that environment, i.e. q=p. Further, let us take k1=k2=k and k3=k4=k'. Then the freq of A and a in generation n were 1−u and u, respectively, in generation n+1 they will be:

[JE:− I will use the # to denote the sub case]

A#(n+1) = (1−u) [p^2+(1−p)^2+2p(1−p)(1−k)]
= (1−u) [1−2p(1−p)k]
a#(n+1) = u[p^2+p(1−p)+(p(1−p)+(1−p)^2) k']
= u[1−(1−p)k']

Therefore:
u #(n+1) = u[1−(1−p)k'] / u[1−(1−p)k']+(1−u)[1−2p(1−p)k]
change in u = u #(n+1)−u #(n) is positive if

u[1−(1−p)k'−u^2[1−(1−p)k']−u(1−u)[1−2p(1−p)k]

is positive, i.e. if

1−(1−p)k'>1−2p(1−p)k

k'>2pk

Thus, as might be expected, which clone is favoured depends not only on the selection coeficients but on the freq' of the environments, and the larger the freq' of environment X the more likely it will pay to canalize for it.

Mendelian Recessive in a diploid
This is the classical paradigm case. In the Neo Darwinist formulation, one assumes a fully recessive gene 'a' in freq 'u'. Then the array of zygotes
in generation n is (1−u)^2 AA, 2u(1−u)Aa, and u^2 aa. In generation n−1 this will be changed to (1−u)^2 AA, 2u(1−u) Aa, u^2(1−k)aa.

In the post−Neo−Darwinist scheme, we have to envisage two environments X and Y in freq' p and 1−p. We can make the same simplifying assumption

that both development and selection occur in these environments in
proportion
to their freq. We have to assign selection coefficients to the phenotypes
derived from all three genotypes in the different combinations of
development
and selection. These would be as follows for a case in which the dominant
gene produces a fully adaptive development, while the recessive produced
canalization for environment X.

Dev' in X Dev' in X Dev' in Y Dev in Y
Sel' in X Sel' in Y Sel' in X Sel' in X

freq'

AA $(1-u)^2$ 1 $1-k$ $1-k$ 1
Aa $2u(1-u)$ 1 $1-k$ $1-k$ 1
Aa $u^2$ 1 $1-k'$ 1 $1-k'$

It is easy to show that the zygotic freq' in the next generation will be:

AA $(1-u)^2$ $[1-2pk(1-p)]$
Aa $2u(1-u)$ $[1-2pk(1-p)]$
Aa $u^2$ $[1-k'(1-p)]$

Whence
$u_{(n+1)}-u_{(n)} = u^2(1-u)[1-k'(1-p)]-[1-2pk(1-p)] / (1-u)^2[1-2pk(1-p)]$
$u^2[1-k'(1-p)]$

This is positive if k' is less than pk.

Alternatively, one may consider the situation in which AA and Aa are
canalized for environment X, while aa produces an adaptive phenotype.
The selection coefficients will be:

Dev' in X Dev' in X Dev' in Y Dev in Y
Sel' in X Sel' in Y Sel' in X Sel'
in X

AA and aa 1 $1-k$ 1 $1-k$

aa 1 $1-k'$ $1-k'$
1

>>From this it turns out that $u_{(n+1)}-u_{(n)}$ is positive if 2pk' is
less than than k. Thus if environment X is the more frequent one
(p greater than 0.5), a gene producing canalization (case 1) can
make its way against an adaptive gene in the face of a less favourable
ratio of selection coefficients than can an adaptive recessive competing

with a canalization dominant.

Conclusions

[..]

What I wished to do was to exhibit a scheme of basic ideas which directs attention towards, rather than away from, the problems which are of most importance for evolutionary theory at the present time. By far the greatest advance in our knowledge of evolution which has occurred in recent years has been the discovery of the enourmous range and variety of genetic variation which is present in natural populations. It seems certain that one of the important determinants of this situation is the fact that such populations exist in heterogeneous environments, so that the applied selection criteria are not the same for all individuals.

[...]

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I aplogize in advance for any errors in the copying of this material. I am happy
to go back and check anything that is incorrect. My scanner cannot scan mathematics so it all had to be done by hand.

I sincerely hope that this posting syimulates discussion in what I cosnsider to
be one of the most important subjects in evolutionary theory: the relationship
between model and theory. I hope that Felsenstein will put to one side the differences between us and honour Waddington by participating in this discussion of one of Waddington's most important contributions.

Regards,

John Edser
Independent Researcher

edser@xxxxxxxxxx

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- ***Follow−Ups***:
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        - *From:* Perplexed in Peoria

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