

ESF Exploratory Workshop on

The New Role of the Extended Phenotype in Evolutionary Biology

SCIENTIFIC REPORT

1. EXECUTIVE SUMMARY

The Extended Phenotype is a major concept in evolutionary biology. Our ESF workshop brought together a highly prestigious group of evolutionary biologists from diverse sub-disciplines to debate the new role of the Extended Phenotype in evolutionary biology following some recent challenges. There were four objectives:

- 1) What, if anything, of Dawkins original (*The Extended Phenotype*, Oxford University Press, 1982) framework needs revision.
- 2) What parts need to be re-formulated to generate more testable predictions?
- 3) Establish a framework for future research
- 4) Decide upon an application strategy for either an ESF follow up initiative or an EU FP7 Early Stage Training Network devoted to interdisciplinary research testing Extended Phenotype theory

Setting

The ESF workshop entitled “The new role of the Extended Phenotype in Evolutionary Biology” took place outside Copenhagen between 2 and 5 November 2008. The workshop was convened and organized by Dr David Hughes (Department of Biology, University of Copenhagen, now at the Museum of Comparative Zoology, Harvard University, dhughes@oeb.harvard.edu) and co-convened by Prof Jacobus J Boomsma (Department of Biology, University of Copenhagen) and Prof Frederic Thomas (CNRS, Montpellier). The workshop was residential at the Rolighed Workshop Centre set in relaxing woodland outside of Copenhagen. Participants arrived the evening of the 2nd and departed the morning of the 5th allowing for two whole days of discussions and three evenings. On the morning of the 5th some participants participated in a roundtable discussion of funding opportunities, held at the Department of Biology, University of Copenhagen.

There were 30 attendees. There were drawn from 9 European countries (Denmark, UK, France, Ireland, Holland, Germany, Switzerland, Italy and Portugal) 2 non-European countries (USA and New Zealand). There were 6 females.

Approach

The workshop was focused on roundtable discussions that were moderated by a chairperson. The discussion followed on from four brief (10 minute) presentations each morning on 4

different topics that set the scene for discussions. All attendees listened to discussions before being divided into one of three groups of 10 that would discuss the topics. Discussions occurred both before and after lunch. At each roundtable discussion there was a rapporteur whose job was to record which topics received either the most attention or were of particular significance. The rapporteurs from each room then discussed in the afternoon with each other and presented their common view to the entire group who once again assembled together. This rapporteur presentation was helpful to orientate delegates for the evening discussions that were informally held over drinks in the evening bar.

The roundtable discussions were a dynamic and highly appreciated forum for discussions because they allowed certain issues to be discussed in depth and clarification to be reached. The problem of course is that individuals cannot be in multiple discussions at once. The role of the rapporteurs was set up to address that. What we also did was mix up the rooms in such a way as all delegates experienced a wide variety of other participants. Finally, all discussions were video recorded and DVD's were edited and sent to their home institutes.

Before delegates arrived they were sent a reading list. This comprised of original papers, reviews, concept and the book *The Extended Phenotype* (signed by the author). The reading list is on a website that is still live <http://www.bi.ku.dk/cse/ep/>

Conclusion

The residential setting, opportunity for discussions, convivial surrounding (food, bar and accommodation) together with the excellent line up of scientists lead to a workshop that all agreed was excellent. Day 1 was marked by an intense atmosphere where delegates sought to understand the meaning of the extended phenotype concept and how it conflicts with emerging themes such as niche construction and how it might relate to community genetics. Day 2 saw a resolution of this conflict when it was generally agreed that it was an issue of semantics and definition rather than a fundamental difference. Thus, a major and quite unexpected advance was made among the delegates.

Having recognized that the debate was potentially resolved attention turned to future activities. All agreed that among the three examples of the extended phenotype (animal architecture, parasite manipulation of behavior and genetic action at a distance) it was parasite manipulation that was most advanced and of greatest potential interest for future

developments. This topic was then selected for future follow-up which took place on the morning of the 5th November during a grant funding roundtable discussion.

2. SCIENTIFIC CONTENT

We gathered together to discuss the **New Role of the Extended Phenotype in Evolutionary Biology**. The Extended Phenotype is a book by Richard Dawkins (1982, Oxford University Press) in which the argument is made that phenotypes can occur beyond the body of the organism. There are three examples

1. Architecture. The artifacts that animals build (nests of birds, fish and insects and the dams of beavers) are phenotypes of the builders. Thus the nest is the extended phenotype.
2. Manipulation. The altered host behaviour that occurs due to the presence of a parasite can be phenotype of the parasite. Thus the behaviour is the extended phenotype.
3. Genetic Action at a Distance. Non-parasitic organisms can alter the behavior other organisms that may be con- or hetero-specific. The altered behavior is the extended phenotype.

As with the conventional view of the phenotype for the definition of extended phenotype we would expect to see both variation in the phenotype and a statistical correlation between this correlation and the fitness of the genes encoding such phenotypes. And phenotype must be heritable. The crucial point Dawkins made in presenting the extended phenotype concept is that it was not a theory or fact but merely a way to view facts. The dam of a beaver is a pile of stick embedded in mud but in some cases it may be useful to view it as a phenotype of the beavers that build it and crucial to their fitness and shaped by natural selection in the same way their rudder like tail has been shaped to aid swimming. If the concept is useful, use it. If it does not illuminate the problem at hand it is not necessary to speak in extended phenotypic terms.

The controversy arises when the concept of the extended phenotype is developed beyond the three examples Dawkins discussed. The **Niche Constructionists** and the **Community Geneticists** are two groups that co-opted the term extended phenotype in ways that some people considered wrong. Niche construction is the process whereby organisms, through their metabolism, their activities, and their choices, modify their own and/or others' niches. It cites

many of the examples of Extended Phenotype such as beavers constructing dams and is reminiscent to the concept of ecosystem engineering where the activities of organisms shape the environment in which they live. What Niche Construction does that is both new and controversial is that it states that our whole understanding of evolutionary theory is incorrect because we do not sufficiently consider the extent to which the Extended Phenotype shapes evolution of the genotypes behind it. That is, after building the dam how also the genetic makeup of the beavers is likely altered. The Niche Construction proponents, such as Marcus Feldman (who attended) argue that their theorem represents an “extended evolutionary theory”, which is a bold statement that has attracted both adherents and detractors. The community geneticists have argued that genes expressed in an organism can have impacts extended far beyond the organism. Originally these effects were phrased as extended phenotypes but that term was not maintained in the literature and this community geneticists is not at odds with the extended phenotype concept.

Resolving the argument

We gathered together to ask:

- 1) What, if anything, of Dawkins original (1982) framework needs revision.
- 2) What parts of the theory need to be re-formulated to generate more testable predictions?

Crucial to answering this was understanding what our definitions of the extended phenotype and niche construction were. There was intense debate on this topic on day 1 which involved Richard Dawkins and Marc Feldman very much in disagreement. Some highly skilled moderation by senior scientists and very stimulating questions and discussions by juniors allowed us to reach the conclusions that the very intense debate that occurred both on day 1 and in the literature that prompted that workshop was **essentially unnecessary**. When it is recognized that the Extended Phenotype concept is a way to view facts rather than a hypothesis (as originally described by Dawkins) then it becomes a much more effective tool and is not an alternative to Niche Construction or a challenge. What our workshop did not effectively address was what utility there is in Niche Construction theorem.

3. ASSESSMENT OF THE RESULTS

Every delegate agreed that the workshop was a major success because it brought together

world class scientists at different levels to discuss a stimulating question of broad significance. Many said it was the most intellectually stimulating meeting they had attended either in years or in their careers. The debates were keen and heated but the end result was one that each person found satisfying. The issue that could be developed further were unanimously decided upon to feature in a special issue of a journal such as the Journal of Evolutionary Biology in which a review article is to be written (by Hughes and the three rapporteurs: Brown, D'Etorre & Linksvayer) and then short responses solicited from delegates were they could clarify their position. This review is in the process of creation.

In addition to this academic output it was decided upon by a sub-set of delegates that pursuing EU wide grant funding initiatives to examine one component of the extended phenotype (parasite manipulation of host behavior) was a sensible immediate funding course of action. Plans are now being carried

4. FINAL PROGRAMME

Session talks are 20 mins with 10 mins for discussion.

Sunday 2 November 2008

afternoon *Arrival of participants at conference centre*

19.30-21.30 *Open Danish Buffet with wine reception* (This will include a presentation that will introduce the participants)

Monday 3 November 2008

Day 1: The Extended Phenotype: its boundary and scope

09.00-09.30 **Opening Remarks**

David Hughes (The Extended Phenotype Workshop: an overview)

09.30-10.30 **Informational overviews of the topics to be discussed**

1. Mike Hansell: Animal architecture
2. Janice Moore: Parasites and animal behaviour
3. Scott Turner: Extended organism
4. Allen Moore: Interacting phenotypes

10.30-11.00 *Coffee break*

11.00-12.30 **Three parallel round table discussions**

10 individuals per discussion in three separate rooms. The purpose of dividing the group is to ensure all participants can contribute to the discussions. On the first day each roundtable group we discussed the boundary and scope of the Extended Phenotype.

12.30-14.00 *Lunch and walk*

14.00-15.30 **Three parallel round table discussions**

(10 individuals per discussion in three separate rooms)

15.30-16.00 *Coffee break*

16.00-17.30 **Round table consensus meetings**

17.30-18.30 **Presentation by rapporteurs**

Each roundtable group will have a pre-appointed rapporteur. Their role is to record, distill and disseminate the key points of their group's discussions. Throughout the day rapporteurs from all three roundtable groups will confer to share notes and coordinate their end of day presentations.

18.30-19.30 **Open Discussion**

19.30-20.30 *Dinner*

20.30-late **Evening bar with open discussions**

Tuesday 4 November 2008

Day 2: The Extended Phenotype: its new role in evolutionary biology

09.00-10.00 **Informational overviews of the topics to be discussed**

1. Sue Healy: Cognition and nest building
2. Mike Wade: Co-evolutionary genetics
3. Steve Stearns: Actions and Ideas

10.00-10.30 *Coffee break*

10.30-12.30 **Three parallel round table discussions**
(10 individuals per discussion in three separate rooms)

12.30-14.00 *Lunch and walk*

14.00-15.30 **Three parallel round table discussions**
(10 individuals per discussion in three separate rooms)

15.30-16.00 *Coffee break*

16.00-17.30 **Round table consensus meetings**

17.30-18.30 **Presentation by rapporteurs**

18.30-19.30 **Concluding statements and steering committee selection**

19.30-20.30 *Dinner*

20.30-late **Evening bar with open discussions**

Wednesday 5 November 2008

Day 3: Follow-up activities

08.30-09.30 *Departure from Conference venue to Copenhagen University*
(non-EU and some EU delegates leave directly)

09.30-12.30 **Planning for EU funding opportunities and other future fund raising activities**

12.30 *Lunch & End of Workshop and Departure*

6. LIST OF PARTICIPANTS

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6. STATISTICAL INFORMATION

Gender: Males- 24, Females-6

Countries : Denmark- 6, UK- 7, France- 3, Ireland- 1, Portugal- 1, Italy- 1, Holland- 1,
Germany-1, Switzerland- 1, USA- 7, New Zealand- 1

Age Bracket

25-40 yrs: 10

40-50 yrs: 6

>50 yrs: 14