EUROPEAN SCIENCE FOUNDATION
SETTING SCIENCE AGENDAS FOR EUROPE

Exploratory Workshop Scheme

Standing Committee for Life, Earth and Environmental Sciences (LESC)

ESF Exploratory Workshop on

# Genotype by Environment Interactions in Sexual Selection

**Falmouth (England), 13-16 July 2010**

**Convened by:**
**Prof. David Hosken, Assoc. Prof. John Hunt and Prof. Nina Wedell**

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# SCIENTIFIC REPORT

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## 1) Executive Summary

The meeting was held over 4 days at the Greenbank Hotel in Falmouth, Cornwall. It was organised by Professor David Hosken, Professor Nina Wedell & Associate Professor John Hunt of the University of Exeter's Centre for Ecology & Conservation on Exeter's Cornwall Campus. The meeting was supported by CEC Professional Staff and students, who did much of the tendering, procurement, costings and acted as support during and after the conference (photocopying, information distribution, IT support, expenses, general help). Their input and efforts went a long way to ensuring the workshop ran smoothly and was such a roaring success

The meeting was attended by 19 academics, including the winner of the prestigeous Sewall Wright Award (2009) of the American Society of Naturalist, Professor Mike Wade. Attendees came from 9 countries (England, Finland, France, Italy, the Netherlands, Scotland, Sweden, Switzerland, & the USA), and all participated in the conference in an open, frank and friendly manner, which meant the workshop was thoroughly enjoyed by all. In fact this was one of the highlights of the conference - all attendees engaged in a very informal, collegial and helpful manner and this made the workshop a tremendously useful event for all that attended. The general atmosphere of the workshop setting (The Greenbank Hotel) also greatly contributed to the general ambiance and positive feel of the meeting, and the setting aside of considerable discussion time both through coffee breaks and the Q&A sessions at the end of talks, greatly facilitated the flow of information and general ferment of ideas.

It was agreed that GxEs are an important, but neglected topic in sexual selection, and they have two major consequences for the field. Firstly, they can help maintain the variation in (male) sexual traits on which (female) choice is focussed. This provides a general solution to the lek paradox, a paradigm that has dominated much thinking in the sexual selection arena. This paradox states that if females are only choosing males for their genes and a small group of males secure all the matings, then the genetic variation on which choice is made will be eroded, and hence there is no longer any genetic variation on which to base choice. However, if there are GxEs for sexual traits, then as with GxE's more generally, selection varies across enviroments and additive genetic variation is maintained. The second issue that was agreed upon was that GxEs can make signals less reliable. For example, if a trait develops in one environment, but selection occurs in another, the trait may no longer reliably provide information about male quality in the second environment. If this were so, then it would be (more) difficult to maintain costly mate choice as the potential benefits of choice would be eroded by this loss of information contain in the signal.

Thus, it can be seen that there is an advantageous component to GxEs for sexual character - genetic variance is maintained - but the flip side is signal reliability may be eroded, potentially obscuring benefits of mate choice. Which of these outcomes is most important will depend on the system and the viscosity of the environment. Indeed, this was another recurring theme

of the conference - population structure has extremely important consequences for the impact of many interactions, be they gene by gene, genotype by environment or indirect genetic effects.

The primary aim of the workshop was to discuss the potential importance of genotype-by-environment interactions (GEIs) and how this could alter our current views of sexual selection. This is an area that has not been fully explored in a sexual selection context, but the conference went a long way towards clarifying important issues and highlighting where we need to go next. We had thought there was some scope for a subsequent European Science Foundation Networking Programme application based on the workshop theme, and we discussed this possibility during the workshop, listing participants who would be interested in such an undertaking. The general feeling was that this was a good idea, and we have begun this process. There was also some discussion on a themed special journal issue or perhaps a book on this theme, and it was agreed that a book was probably the best route and we have had preliminary agreement with a publisher on this.

Overall the workshop was a great success. Our primary objectives were met and some additional benefits/outcomes were also achieved. We have now identified a great core group of scientist with whom we can cooperate to take this theme forward. Their interests and skills are broad, but with enough overlap that a joint venture could really reap rewards and answer the questions that this ESF funded meeting identified. As the final part of this summary we would therefore like to thank the LESC for their generous support of the workshop. It has been tremendously hepful for us, allowing us to network with leaders in this field, and the investment will reap further reward as we begin to more fully unravel the causes and consequences of GxE in sexual selection.

## 2. Scientific content of the event

The overarching theme was genotype by environment interactions in sexual selection, but the variety of talks and approaches to this general topic was fairly broad. Mike Wade (USA) began with a general talk about GxE and interactions generally. He emphasised that environmental viscosity was likely to have a very important impact on the outcomes of interactions, and population structure will be variable. There was substantial discussion of this issue which is part of the largely unresolved Wright-Fisher debates during the Darwinian Synthesis that brought Mendelian genetics together with Darwinian selection. Jerome Goudet (Switzerland) then spoke to us about a computor platform he has developed to explore quantitative traits *in silico*. This programme could be easily modified to explore sexual sélection GEIS, but this is still in its infancy. Much of the discussion focussed on details of the programme and how it could be used in sexual selection studies, with talk of PhD student exchange between England and Switzerland to explore this. Hanna Kokko then discussed the good and the bad of GxE.

This explicitly focussed attention on the tension between the maintenance of genetic variation and the problems of signal reliability. Kokko suggested that empiricists should focus on testing models which generated substantial discussion as it was felt that models were amenable to testing - no biological system comes close to approximating any particular model. Michael Greenfield (France) then discussed the extraordinary work conducted by him and his team on GxE in waxmoths. This is one of the few systems where GxE in sexual selection has been investigated in depth and the insights from the work, together with Greenfield long ruminations on the issue, are breathtaking. One issue that has subject of some discussion was the potential for GEI to disrupt Runaway by breaking linkage between preference and trait, and the posibility that Fisherian effects *in toto* can be disrupted. Alex Roulin (Switzerland) then discussed his work on owls. This is a large body of work on a free-living bird that has taken many years of data collection. He discussed the pleiotropic effects of the POMC gene and importantly how ontogenetic conflcit could maintain some signal reliability even with GEI for male traits. This topic needs more thought. Susie Mills (France) then discussed her work on voles. She reported that there were substantial GxE for male dominance that may be mediated by testosterone. Luc Bussiere (Scotland) then discussed work done on dungflies and how stress may be important. His worked showed that there were GEIs for most of the traits measured, but the strength of the GEI was trait and environment specific and he suggested that using multiple and realistic stresses was the best expérimental approach. Mike Ritchie then closed off day one with a discussion of *Drosophila*. This was an example of a small viscous world with substantial GxE, ExE and gxg. In fact in some fies about 50% of the Vp in behaviour was due to GxE, but perhaps surprisingly, less than 1% of genes contribute to that. Andrew Pomiankowski (England) kicked-off day 2 with a discussion of condition dependence and GxE. He emphasised the need to disentangle mate sampling and preference. There was much discussion of why high condition females mated more not less. Ted Morrow (Sweden) then talked about the use of hemiclones to investigation GxE, and an analysis of sperm length displayed the utility of this approach. A main points of discussion was why gonads showed little evidence of ontogenetic conflict. Lotta Sunstrom (Finland) then discussed work with ants and how Ne was low becuase colonies not individuals are the reproductive unit. One major point of interest was the degree of inbreeding depression in these haplo-diploids. Ulrika Candolin (Finland) then discussed the effects of eutrophication on male signal honesty. As water become more turbid male signals become less reliable because male-male competition is reduced. There was discussion of possible aging effects of increased selection at late life. Matt Robinson (Sweden) then discussed the use of animal models in investigating sexual selection in nature. His work suggested there was no net sexual selection on flycatcher feathers and potential problems with non-expermental approaches were discussed. Daniel Rankin (Switzerland) discussed how local versus global competition can effect sexual selection and sexual conflict and how relatedness can be one important parameter in conflict resolution. Andrea Pilastro then discussed post-copulatory sexual selection in guppies. Evidence that sperm

number was negatively associated with siring success was presented. The meeting was closed by John Hunt (England) who presented indirect genetic effects models developed primarily by Moore, Brody & Wolf. It became apparent that one key parameter in these models depends largely on population viscosity and this could in some sense be thought of as equivalent to Hamilton's r. A long discussion of psi then followed. Shortly thereafter a group discussion of the major outcomes of the workshop occurred and the formal aspects of the meeting were then closed.

## 3. Assessment of the results, contribution to the future direction of the field, outcome.

As stated above, the major results of the meeting were the hightened awareness of the good and bad of GxE for sexual selection and the importance of population structure. This second point was highlighted in a large number of ways and the importance of psi, a key parameter in indirect genetic effects models that depends on environmental/population viscosity, became clear to many as a direct result of the discussions at the workshop. There was also a new awareness of the importance to focus on GxE in future studies. Future work plans include a book based on the workshop's theme, and a Research Network Grant submission. The book planning is already at an advanced stage.

## 4. Final programme

### Tuesday 13th July 2010

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| Afternoon | *Arrival* |
| *18.00* | *Get-together, social event, informal (Greenbank Hotel)* |
| *19.30* | *Dinner* |

### Wednesday 14th July 2010

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| 09.00-09.25 | **Greetings** |
| 09.25-09.40 | **Welcome**<br>**David Hosken** (University of Exeter) |
| **09.40-12.30** | **Morning Session** |
| 09.40-10.40 | **Presentation 1 "Plastic male phenotypes, sexual selection and female mate choice"**<br>**Mike Wade** (Univeristy of Indiana, Bloomington, USA) |
| 10.40-11.10 | **Presentation 2 "QuantiNEMO: an individual-based program for the analysis of quantitative traits"**<br>**Jerome Goudet** (University of Lausanne, Lausanne, Switzerland) |
| 11.10-11.30 | *Coffee / Tea Break* |

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| 11.30-12.00 | **Presentation 3 “So is the net effect positive or negative? It depends….”**<br>**Hanna Kokko** (University of Helsinki, Helsinki, Finland) |
| 12.00-12.30 | **Discussion** |
| 12.30-14.00 | *Lunch* |
| **14.00-18.30** | **Afternoon Session** |
| 14.00-14.30 | **Presentation 1 “GEI, signal reliability, and speciation”**<br>**Mike Greenfield** (Université François Rabelais de Tours, Tours, France) |
| 14.30-15.00 | **Presentation 2 “GxE and signalling adaptations to alternative habitats”**<br>**Alex Roulin** (University of Lausanne, Lausanne, Switzerland) |
| 15.00-15.30 | **Presentation 3 “Genotype by environment interactions and signal reliability in the bank vole”**<br>**Suzanne Mills** (Université de Perpignan via Domitia, Perpignan, France) |
| 15.30-16.00 | *Coffee / tea break* |
| 16.00-16.30 | **Presentation 1 “Selection, sex-specific GEI and stress resistance”**<br>**Luc Bussiere** (University of Stirling, Stirling, Scotland) |
| 16.30-17.00 | **Presentation 2 “GxE & Drosophila mojavensis”**<br>**Mike Ritchie** (St Andrews University, St Andrews, Scotland) |
| 17.00-18.30 | **Discussion** |
| 19.00 | *Dinner* |

## Thursday 15th July 2010

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| **09.00-13.00** | **Morning Session** |
| 09.00-09.30 | **Presentation 1 “Condition-dependent female sexual selection”**<br>**Andrew Pomiankowski** (UCL, London, England) |
| 09.30-10.00 | **Presentation 2 “Putting the H into GxE”**<br>**Ted Morrow** (Uppsala University, Uppsala, Sweden) |
| 10.00-10.30 | **Presentation 3 “Genetics and trade-offs in ants”**<br>**Lotta Sundstrom** (University of Helsinki, Helsinki, Finland) |
| 10.30-11.00 | *Coffee / Tea Break* |
| 11.30-12.00 | **Presentation 4 “Is plastic courtship beneficial in a changing world?”**<br>**Ulrika Candolin** (University of Helsinki, Helsinki, Finland) |
| 12.00-12.30 | **Discussion** |
| 12.30-14.00 | *Lunch* |
| **14.00-18.30** | **Afternoon Session** |
| 14.00-14.30 | **Presentation 1 “Ecological influences on sexual selection drives speciation in flycatchers”**<br>**Matt Robinson** (Uppsala University, Uppsala, Sweden) |
| 14.30-15.00 | **Presentation 2 “Kin selection and the evolution of sexual conflict”**<br>**Daniel Rankin** (University of Zurich, Zurich, Switzerland) |
| 15.00-15.30 | *Coffee / Tea Break* |
| 15.30-16.00 | **Presentation 1 “QG of post-copulatory sexually selected traits in the guppy. Why an environmental perspective is needed”**<br>**Andrea Pilastro** (University of Padua, Padua, Italy) |

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| 16.30-17.00 | **Presentation 1 "Interacting phenotypes: indirect genetic effects and evolution"**<br>**John Hunt** (University of Exeter, Exeter, England) |
| 17.00-18.30 | **Discussion on follow-up activities / networking / collaboration** |
| 19.00 | *End of Workshop Dinner* |

## Friday 16th July 2010

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| **09.30** | *End of Workshop and departure* |

## 5. Final list of participants

1. Bussiere L (Stirling, Scotland)
2. Candolin U (Helsinki, Finland)
3. Goudet J (Lausanne, Switzerland)
4. Greenfield M (Tours, France)
5. Hosken DJ (Exeter, England)
6. Hunt J (Exeter, England)
7. Kokko H (Helsinki, Finland)
8. Mills S (Perpignan, France)
9. Morrow T (Uppsala, Sweden)
10. Pilastro A (Padua, Italy)
11. Pominakowski A (London, England)
12. Rankin D (Zürich, Switzerland)
13. Ritchie M (St Andrews, Scotland)
14. Robinson M (Uppsala, Sweden)
15. Roulin A (Lausanne, Switzerland)
16. Sundstrom L (Helsinki, Finland)
17. Veen T (Haren, The Netherlands)
18. Wade M (Indiana, USA)
19. Wedell N (Exeter, England)

## 6. Statistical information on participants

*Age:*
20-30 = 5
30-40 = 3
40-50 = 9
50+ = 3

*Sex:*
F = 5
M = 14

*Country*
England = 4, Finland = 3, Switzerland = 3, France = 2, Scotland = 2, Sweden = 2, Italy = 1, The Netherlands = 1, USA = 1