



ASAB Winter Conference • 5–6 December 2013



# THE EVOLUTION OF BEHAVIOURAL MECHANISMS

## Thursday 5 December

|                    |                             |  |
|--------------------|-----------------------------|--|
| <b>09.30–10.00</b> | <b>coffee &amp; posters</b> |  |
| 10.00–10.10        | <b>The MAD group</b>        | Introduction to the meeting  |
| 10.10–11.00        | <b>Melissa Bateson</b>      | <b>PLENARY</b><br>Memory of hunger: cognitive scars of early-life adversity in European starlings?                 |
| 11.00–11.20        | <b>Willem Frankenhuis</b>   | When does natural selection favour sensitive periods in development?   |
| 11.20–11.40        | <b>Alex Kacelnik</b>        | Paradoxical preferences for low probability of reward: how adaptive mechanisms can have costly consequences        |
| 11.40–12.00        | <b>Kate Morgan</b>          | Decision making in context: comparing the choices of humans and animals  |
| 12.00–12.20        | <b>Vivek Nityananda</b>     | Bumblebee visual search for multiple learned target types  |
| <b>12.20–14.00</b> | <b>lunch &amp; posters</b>  |  |
| 14.00–14.20        | <b>Dave Shuker</b>          | Constraints on adaptive sex allocation behaviour   |
| 14.20–14.40        | <b>Jarl Giske</b>           | Effects of the emotion system on adaptive behaviour  |
| 14.40–15.00        | <b>Dani Sulikowski</b>      | The function of mechanism: linking cognition to foraging ecology   |
| 15.00–15.20        | <b>Jayden van Horik</b>     | Behavioural flexibility in parrots   |
| 15.20–15.40        | <b>Robert Biegler</b>       | Relational complexity  |
| <b>15.40–16.10</b> | <b>tea &amp; posters</b>    |  |
| 16.10–17.00        | <b>Reuven Dukas</b>         | <b>PLENARY</b><br>Social information use in fruit flies: mechanisms and functions                                  |
| 17.00–17.20        | <b>Frederic Mery</b>        | Diffusion of social information within <i>Drosophila</i> group : natural genetic variation for social transmission |
| 17.20–17.40        | <b>Neeltje Boogert</b>      | Pre- and post-natal stress have opposing effects on social information use   |
| 17.40–18.00        | <b>Rui Oliveira</b>         | Searching for the social brain: neural and molecular mechanisms of social learning in zebrafish                    |
| <b>18.00–19.30</b> | <b>wine &amp; posters</b>   | <i>see overleaf for posters</i>  |

Chairs: Tim Fawcett (10.10–12.20), Sophie Mowles (14.00–15.40), Andy Higginson (16.10–18.00)

## Friday 6 December

|                    |                             |  |
|--------------------|-----------------------------|--|
| <b>09.00–09.50</b> | <b>coffee &amp; posters</b> |  |
| 09.50–10.40        | <b>Simon Laughlin</b>       | <b>PLENARY</b><br>Ascending Shannon's slopes: how the cost of information constrains brains  |
| 10.40–11.00        | <b>Gerit Pfuhl</b>          | Complex behaviour despite a simple ear   |
| 11.00–11.20        | <b>Thomas Hills</b>         | Animal foraging and the evolution of attentional control   |
| 11.20–11.40        | <b>Oren Kolodny</b>         | Foraging challenges in statistically structured environments give rise to learning mechanisms which may account for 'advanced cognitive abilities' |
| 11.40–12.00        | <b>Alexander Kotrschal</b>  | From artificial selection to transcriptomics: the cognitive benefits of, and the gene responsible for, a large brain                               |
| 12.00–12.20        | <b>Joe Woodgate</b>         | What mechanisms underlie visually-guided navigation in foraging wood ants ( <i>Formica rufa</i> )?   |
| <b>12.20–14.00</b> | <b>lunch &amp; posters</b>  |  |
| 14.00–14.20        | <b>Sophie Mowles</b>        | The costs of courtship: using physiology and performance to understand what females want   |
| 14.20–14.40        | <b>Michele Johnson</b>      | The evolution of muscle physiology and social behaviour in Caribbean <i>Anolis</i> lizards   |
| 14.40–15.40        | <b>Marlene Zuk</b>          | <b>NIKO TINBERGEN LECTURE</b><br>The role of behaviour in the establishment of novel traits  |
| <b>15.40–16.10</b> | <b>tea &amp; posters</b>    |  |
| 16.10–16.30        | <b>Arnon Lotem</b>          | Evolution of learning and levels of selection: a lesson from avian parent–offspring communication  |
| 16.30–16.50        | <b>Patricia Lopes</b>       | Socially-induced plasticity of sickness behaviours and its neuroendocrine basis  |
| 16.50–17.10        | <b>Michal Arbilly</b>       | Complex interactions between individual and social learning processes shape their evolution  |
| 17.10–17.30        | <b>Magda Teles</b>          | Socially driven changes in neural plasticity mediate behavioural flexibility   |
| 17.30–17.50        | <b>Luc-Alain Giraldeau</b>  | Non-social learning in a social context  |
| <b>17.50</b>       | <b>close</b>                |  |

Chairs: Pete Trimmer (09.50–12.20), Dani Sulikowski (14.00–14.40), Willem Frankenhuis (16.10–17.50)

## Posters

|    |                                 |   |
|----|---------------------------------|---|
| 1  | <b>Christian Agrillo</b>        | Evidence of multiple cognitive systems underlying numerical abilities of vertebrates  |
| 2  | <b>Stefan Leitner</b>           | Environmental and genetic control of brain and song structure in the zebra finch  |
| 3  | <b>Anne Salvanes</b>            | Environmental enrichment promotes neural plasticity and cognitive ability in fish   |
| 4  | <b>Julia Purser</b>             | Costly responses to acoustic stressors: underlying physiology, psychology and flexibility?  |
| 5  | <b>Lorenz Gygax</b>             | Mood–emotion interaction effects on behavioural and brain reactions of sheep exposed to video images of social interactions                       |
| 6  | <b>João Messias</b>             | The role of dopaminergic system in the modulation of the Indo-Pacific bluestreak cleaner wrasse <i>Labroides dimidiatus</i> cooperative behaviour |
| 7  | <b>Cecilia Wikström</b>         | Behavioural and molecular responses to a social challenge in a cooperative breeder reared in different social environments                        |
| 8  | <b>Claudia Kasper</b>           | Behavioural and genomic responses of a cooperatively breeding cichlid to a helping task   |
| 9  | <b>David Baracchi</b>           | Nestmate recognition in Stenogastrinae wasps: visual and chemical information are not integrated in a multimodal sensory cue                      |
| 10 | <b>Cedric Tan</b>               | Sex-specific response to the familiarity of mates, and the role of olfaction  |
| 11 | <b>Zineb El Filali</b>          | Mass spectrometric study of the peptidergic neurotransmission regulating male mating in a mollusc, <i>Lymnaea stagnalis</i>                       |
| 12 | <b>F-X Dechaume-Moncharmont</b> | Scramble competition severely impairs mate choosiness   |
| 13 | <b>Thomas Hoffmeister</b>       | What makes a forager leave a resource patch? Confronting models with reality  |
| 14 | <b>Benja Fallenstein</b>        | Heritable personality traits probably aren't correct Bayesian priors  |
| 15 | <b>Noa Truskanov</b>            | Active search and self-experience mediate the success of both social and individual learning in house sparrow fledglings                          |
| 16 | <b>Thomas Hesselberg</b>        | Behavioural flexibility and learning in orb spiders   |
| 17 | <b>Erika Dawson</b>             | Learning by observing others arises through simple associations in an insect model  |
| 18 | <b>Barbara Webb</b>             | Not so simple associative learning  |
| 19 | <b>Kit Longden</b>              | Internal state modulation of visual motion processing in walking blowflies  |
| 20 | <b>Adrian Bell</b>              | Locusts show handedness during goal-orientated movements  |

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Organised by  
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## TALKS

### PLENARY 1

Thu 10.10–11.00

#### Memory of hunger: cognitive scars of early-life adversity in European starlings?

Melissa Bateson (melissa.bateson@ncl.ac.uk)  
Newcastle University

People who experience harsh early environments are more likely to develop affective disorders and behavioural problems such as addiction as adults, suggesting a cognitive style involving increased pessimism and impulsivity. People with these traits also have shorter telomeres in their leukocytes, suggesting that telomere attrition is a biomarker of cumulative psychosocial stress. The human evidence for these effects is correlational, and to show that there is a causal relationship between early-life stress, telomere attrition and adult cognition an experimental animal model is required. We have developed the European starling (*Sturnus vulgaris*) as a novel model for studying these relationships. Starlings are long-lived, wild animals in which we can manipulate the early environment easily, and for which we have already developed many cognitive measures. I will present data from a cohort of siblings that were raised in nests where they faced either high or low competition for food. We show that increased competition is associated with increased developmental telomere attrition. We also find cognitive differences in adults including increased impulsivity, increased expectation of reward and decreased dietary selectivity. This suite of traits is characteristic of hungry animals, but at the time of our experiments, the birds did not differ in size, weight, or deprivation. Thus, the birds that had faced early food competition behaved as if hungrier than their siblings, even though their current states were ostensibly the same. Our results demonstrate long-term effects of early experience on personality variation, and establish telomere attrition as a biomarker of condition. I discuss whether our findings represent an example of adaptive developmental plasticity.

### TALK 1

Thu 11.00–11.20

#### When does natural selection favour sensitive periods in development?

Willem Frankenhuis (wfrankenhuis@gmail.com)  
Radboud University Nijmegen  
with Karthik Panchanathan

Models of phenotypic plasticity tend to ignore that development is often an incremental process. In previous work, we examined how natural selection might shape ontogenies when gradual phenotypic construction trades off with sampling cues to the environmental state. In this talk, we present a follow-up model in which sampling and specialisation are not mutually exclusive: individuals sample throughout their lifespan, while simultaneously constructing their phenotypes. Organisms have the option of reversing their development, at some cost,

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which is a function of the number of increments developed in the suboptimal direction. We use stochastic dynamic programming to compute optimal policies for a range of evolutionary environments. We explore different prior probability distributions of environmental states, values of information, functions mapping correct specialisations to fitness gains, and functions mapping incorrect specialisations to fitness losses (costs of reversing). Results show that in some developmental periods, organisms forego phenotypic construction and only sample; organisms may continue along the same developmental trajectory even when new information informs them the associated environmental state is unlikely (implying a sensitive window earlier in ontogeny); and individual differences in susceptibility to information may arise from differences in sampling histories, specifically the degree of consistency of the sampled cue set.

### TALK 2

Thu 11.20–11.40

#### Paradoxical preferences for low probability of reward: how adaptive mechanisms can have costly consequences

Alex Kacelnik (alex.kacelnik@zoo.ox.ac.uk)  
University of Oxford  
with Tiago Monteiro & Marco Vasconcelos

Everything else being equal, animals prefer high to low probabilities of reward, early to late rewards, and larger to smaller rewards, but when everything else is not exactly equal, these expectations are often violated, and animals display apparently paradoxical preferences. We argue that such cases are important in revealing the mechanisms controlling preferences and choices, and discuss an experimental protocol in which starlings and other species prefer an option with lower reward probability but earlier availability of outcome information, thus systematically losing the majority of available rewards but spending less time uncertain. We consider three mechanistic interpretations (uncertainty aversion, local contrast and Pavlovian conditioning), discuss their merits and relate the findings to the tension between sequential decisions in the wild and simultaneous decisions in the laboratory.

### TALK 3

Thu 11.40–12.00

#### Decision making in context: comparing the choices of humans and animals

Kate V. Morgan (km745@st-andrews.ac.uk)  
University of St Andrews  
with Ronan Kearney, T. Andrew Hurly & Susan D. Healy

Contrary to rational choice theory, the choices made by animals and humans can be altered by the addition of inferior options to choice sets. Although changes in preference are observed in both humans and animals it is not clear whether the mechanisms that may underlie these changes are the same. Here we attempted to assess the similarities in these mechanisms by conducting

comparable choice experiments in both humans and hummingbirds: the human participants assessed the health of faces while wild rufous hummingbirds chose among options that varied in energetic return. The addition of poorer options to the choice sets changed the decisions made by both the human participants and the hummingbirds. However, while there were similarities in their patterns of decision making, the hummingbirds and the humans also differed in how their preferences were affected by the inclusion of poorer options to their choice sets. These differences in the responses to the addition of poorer options may be due to differences in preference functions underpinning the choices or because the decision making mechanism responsible for the irrational decision making of humans and animals differs.

#### TALK 4 Thu 12.00–12.20

### Bumblebee visual search for multiple learned target types

Vivek Nityananda (vivek.nityananda@ncl.ac.uk)  
Queen Mary University of London  
Newcastle University  
with Jonathan G. Patrick

Human visual search is well studied but we know comparatively little about similar capacities in non-human animals. It is sometimes assumed that animal visual search is restricted to a single target at a time. In bees, for example, this limitation has been evoked to explain flower constancy, the tendency of bees to specialise on a single flower type. But is this behaviour limited by memory constraints or can bees choose flexibly once they learn different targets? Few studies have investigated bee visual search for multiple target types after extended learning and controlling for prior visual experience. We trained colour-naive bumblebees in separate discrimination tasks to recognise two rewarding colours in block training sessions. We tested them with both colours simultaneously in the presence of distracting colours to examine whether and how quickly they switched between target colours. We found that bees switched between visual targets quickly and often. The median time taken to switch between targets was shorter than known estimates of how long traces last in bees' working memory suggesting that their capacity to recall more than one learned target was not restricted by working memory limitations. Bees can thus switch between multiple learned targets flexibly and quickly.

#### TALK 5 Thu 14.00–14.20

### Constraints on adaptive sex allocation behaviour

David M. Shuker (david.shuker@st-andrews.ac.uk)  
University of St Andrews

Sex allocation behaviour has provided evolutionary biologists with some of their most spectacular successes in terms of quantitative tests of theory. This is particularly true for sex allocation under Local Mate Competition (LMC). LMC arises when related males (such as brothers)

compete amongst themselves for access to mates, and theory predicts extremely female-biased sex ratios when sexual competition is purely amongst kin. Such predictions have been borne out across many different species in many different LMC contexts. As such, is there anything left to learn about sex allocation in these species? Despite the success of LMC theory, we still know virtually nothing about how animals optimally allocate sex under LMC conditions. In this talk I will explore constraints on adaptive sex allocation in the wasp *Nasonia vitripennis*. Female *Nasonia* follow the predictions of LMC theory in many contexts, often with remarkable sophistication. However, their behaviour is not always "perfect", for instance they fail to produce the predicted sex ratios when kin- and species-discrimination is required. I will describe recent genetic and genomic approaches that are uncovering the mechanistic basis of sex allocation in *Nasonia* and ask to what extent can behavioural mechanisms explain departures from optimal behaviour.

#### TALK 6 Thu 14.20–14.40

### Effects of the emotion system on adaptive behaviour

Jarl Giske (jarl.giske@bio.uib.no)  
University of Bergen  
with Sigrunn Eliassen, Øyvind Fiksen, Per J. Jakobsen, Dag L. Aksnes, Christian Jørgensen & Marc Mangel

A central simplifying assumption in evolutionary behavioural ecology has been that optimal behaviour is unaffected by genetic or proximate constraints. Observations and experiments show otherwise, so that attention to decision architecture and mechanisms is needed. In psychology the proximate constraints on decision-making and the processes from perception to behaviour are collectively described as the emotion system. We specify a model of the emotion system in fish, including sensory input, neuronal computation, developmental modulation, and a global organismic state, which restricts attention during decision-making of behavioural outcomes. The model further includes food competition, safety in numbers, and a fluctuating environment. We find that emergent strategies in evolved populations include common emotional appraisal to sensory input related to fear and hunger, and frequency-dependent rules for behavioural responses. Focused attention is at times more important than spatial behaviour for growth and survival. Spatial segregation of the population is driven by personality differences. By coupling proximate and immediate influences on behaviour with ultimate fitness consequences through the emotion system, this approach contributes to a unified perspective on the phenotype, by integrating effects of the environment, genetics, development, physiology, behaviour, life history and evolution.

## TALK 7

Thu 14.40–15.00

**The function of mechanism: linking cognition to foraging ecology**

Danielle Sulikowski (danielle.sulikowski@ymail.com)  
 Charles Sturt University  
 with Darren Burke

Noisy miners (an Australian honeyeater) feed on both nectar and invertebrates. The distributions of these two food resources differ: nectar is a static, visually cued resource that depletes and replenishes in a predictable way while invertebrates are cryptic and mobile. If the cognitive mechanisms that underpin foraging have been adapted to increase foraging efficiency, we might predict the competing demands of nectar and invertebrate food source to result in (at least) two sets of divergent mechanisms. Here, we present evidence of two such divergent systems, each apparently triggered by the proximate ingestion (or expectation) of the relevant food type. The nectar system appears to be less flexible than the invertebrate system, but may have a longer lasting memory for high-resolution spatial information. We are also investigating whether these two systems differ in the extent to which they integrate information observed over time versus the extent to which they produce behaviour based only on the most recent information gleaned.

## TALK 8

Thu 15.00–15.20

**Behavioural flexibility in parrots**

Jayden O. van Horik (j.van-horik@qmul.ac.uk)  
 Queen Mary University of London  
 with Nathan J. Emery

We presented red-shouldered macaws (*Diopsittaca nobilis*) and black-headed caiques (*Pionites melanocephala*) with a series of Serial Reversal Learning and Means-End transfer tasks to assess whether cognitive or associative mechanisms underlie capacities for behavioural flexibility. A Serial Reversal Learning paradigm revealed that parrots were capable of using flexible learning strategies, such as rule abstraction, to rapidly respond to alternating reward contingencies, and that their behaviours were not constrained by associative mechanisms, such as conditioning and extinction. A new method for testing means-end reasoning, the Trap-Gaps task, required substantial experience for subjects to learn to discriminate between pulling food-trays through gaps, while attending to the respective width of the gaps and size of the trays. Yet, some individuals spontaneously solved a novel transfer task, suggesting capacities for generalised learning. The performances of these birds concurs with findings from other relatively large brained species, such as corvids and apes, suggesting that large brains afford higher-order cognitive mechanisms that allow animals to rapidly respond to novel experiences by generalising previously learned information. Moreover, as such abilities are shared among distantly related species, these findings also suggest that certain socio-ecological selection pressures may have resulted in a convergent evolution of flexible learning mechanisms.

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## TALK 9

Thu 15.20–15.40

**Relational complexity**

Robert Biegler (robert.biegler@svt.ntnu.no)  
 Norwegian University of Science & Technology  
 with Gerit Pfuhl

Halford et al. (1998) proposed that one factor that limits reasoning ability is the complexity of the representations that can be built. Halford et al. define complexity in a manner analogous to the difference between t-tests or simple discriminations, two-way interactions or logical XOR or biconditional discriminations, three-way interactions, and so on. Our review of the literature indicates that *Drosophila* is limited to simple discriminations, bees, pigeons, rats and baboons can solve biconditional discriminations, but have not been tested with more difficult problems. Humans are limited to problems equivalent to four-way or five-way interactions. We report that one jackdaw can solve a problem as complex as a three-way interaction. We also find that humans solving either the same or related tasks can simplify the problem in a way not covered by several measures of the complexity of discriminations. To the extent that our task captures the limits of the complexity of representations, it provides an absolute measure of at least one factor that limits reasoning.

## PLENARY 2

Thu 16.10–17.00

**Social information use in fruit flies: mechanisms and functions**

Reuven Dukas (dukas@mcmaster.ca)  
 McMaster University

There has recently been increased interest in establishing simple, tractable model systems for research on the evolution and neurogenetic mechanisms of social information use. I will first discuss the life history traits favouring the evolution of social learning. Then I will detail research from my lab on social attraction and social learning in larval and adult fruit flies, the cues that mediate social information use and the value of such information. Finally, I will describe preliminary work on the dynamics of spontaneous social behaviour in fruit fly larvae during their development from hatching to pupation and the function of such behaviour.

## TALK 10

Thu 17.00–17.20

**Diffusion of social information within *Drosophila* group: natural genetic variation for social transmission**

Frederic Mery (frederic.mery@legs.cnrs-gif.fr)  
 CNRS, Gif-sur-Yvette  
 with M. Battesti, C. Pasquaretta, C. Moreno, D. Joly, C. Wicker & C. Sueur

How social information can spread and be maintained within a group has been a central question in behavioural ecology. Recent studies have found that *Drosophila melanogaster* can use social information to select for specific oviposition medium. Naive female flies modify

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their oviposition medium choice after having interacted with demonstrator flies which have been trained to prefer one specific medium. Here we present the first evidence of genetic variation for social transmission using the well described genetic natural polymorphism on foraging gene. The foraging gene encodes a cGMP-dependent protein kinase (PKG), and natural allelic variation results in the 'rover' (*forR*) and 'sitter' (*fors*) behavioural variants that differ in PKG activity levels. We performed a series of social transmission experiments and show that, if rover flies can acquire information from trained rovers or trained sitters without discrimination, naive sitters are selective on the choice of the source of information and only acquire information from trained sitters. We present evidence of a role of the cuticular hydrocarbon profile produced by the flies on social transmission. Our results provide perspectives on the study of the genetic and socio-environmental factors affecting social transmission with the integration of experimental approach, social network analysis and modelling.

**TALK 11** Thu 17.20–17.40

### Pre- and post-natal stress have opposing effects on social information use

Neeltje Boogert (njboogert@gmail.com)

University of St Andrews

with Cedric Zimmer & Karen A. Spencer

Theoretical models of social learning predict that animals should copy others in variable environments where resource availability is relatively unpredictable. Short-term exposure to unpredictable conditions in adulthood has been shown to encourage social learning. However, virtually nothing is known concerning whether and how conditions during development affect social information use. Unpredictable food availability increases levels of the stress hormone corticosterone (CORT). In birds, CORT can be transferred from the mother to her eggs, and have downstream behavioural effects. We tested how pre-natal CORT elevation through egg injection, and chick post-natal development in unpredictable food conditions, affected social information use in adult Japanese quail (*Coturnix japonica*). Pre-natal CORT exposure encouraged quail to copy the foraging decisions of demonstrators in video playbacks, whereas post-natal food unpredictability led individuals to avoid the demonstrated food source. An individual's exposure to stress and uncertainty during development can thus affect its use of social foraging information in adulthood. However, the stressor's nature and developmental timing determine whether an adult will tend to copy conspecifics or do the opposite. Developmental effects on social information use might thus help explain individual differences in social foraging tactics and leadership.

**TALK 12** Thu 17.40–18.00

### Searching for the social brain: neural and molecular mechanisms of social learning in zebrafish

Rui F. Oliveira (ruiol@ispa.pt)

ISPA – Instituto Universitário

with Julia Pinho, Rodrigo Abreu, João Lopes & Marisa Fernandes

Opportunities to use public information (i.e. social learning) are ubiquitous in social environments. Therefore, it has been hypothesised that group living has promoted the evolution of social learning skills. A major difference between social and asocial learning is that prediction error, which is considered a learning signal, is not directly available in the former. However, it is still an open question if social learning relies on a newly evolved learning module that deals with this particular type of learning, or if on the contrary the mechanisms underlying social learning are the same as those involved in general purpose learning. It has also been proposed that the difference may rely not on the learning mechanism itself, but rather on attentional processes that make social information available. In this study we address these two questions by: (1) characterising the behavioural, neural and molecular mechanisms underlying a social and an equivalent asocial learning task in zebrafish; for this purpose an observational fear conditioning paradigm was contrasted with a classical fear conditioning paradigm. (2) developing a task to study social attention in zebrafish; for this purpose fish observed a pair of non-interacting conspecifics, a pair of interacting conspecifics or an empty tank, and their engagement with the stimuli was measured using a homemade video-tracking system. Behavioural data show similar learning rates in the two learning tasks but higher attention rates towards interacting conspecifics. Brain transcriptome data show differential expression of a small number of genes in the attention task, which are thus candidates to be involved in attentional processes in zebrafish. These results will be discussed in the scope of the hypothesis of brain modularity for social information.

**PLENARY 3** Fri 09.50–10.40

### Ascending Shannon's slopes: how the cost of information constrains brains

Simon Laughlin (sl104@cam.ac.uk)

University of Cambridge

As a brain evolves, natural selection balances the cost of investing in information against its benefits, within the context of fitness. Neurobiologists generally study the bright side of investment—specializations that adapt an animal to its niche by improving its ability to process information. I consider the dark side—the costs that drive performance down. I make the case that a brain's ability to process information is constrained by space, materials and energy and that brains have evolved to use these resources efficiently. Having discussed the contentious

issue of where, when and why information in bits is a useful measure of performance, I consider Shannon's slopes. The gradients of curves relating information to cost decrease as performance and cost increase. This enforcement of the Law of Diminishing Returns drives down performance by punishing excess capacity. The punishment is made more severe by brain's winning technology, cell biology. I conclude that the pressure to use resources efficiently guides brain evolution, and we can start to weigh costs and benefits.

**TALK 13**

Fri 10.40–11.00

**Complex behaviour despite a simple ear**

Gerit Pfuhl (gerit.pfuhl@ntnu.no)

*Norwegian University of Science & Technology*

with Mikhail K. Zhemchuzhnikov, Xin-Cheng Zhao &amp; Bente Berg

Sensory systems are adapted to the ecological need. A typical example is the lepidopteran ears, which have evolved primarily for detecting the sound of hunting bats. In heliothine moths the ear has two auditory neurons only. Still, the moths do not show a rigid behaviour upon exposure to bat calls. When flying in a pheromone plume, indicating the vicinity of a receptive female, the male moth may pursue the odour trace upwind despite hearing a bat call. Recent research has indicated that the flexible behavioural responses caused by simultaneous input from odour and sound are linked to distinct neural processes taking place in the brain. Particularly interesting in this context is our identification of a centrifugal neuron transferring auditory information to seemingly all second-order olfactory neurons in the heliothine moth brain. Also, our recent findings indicate that the auditory information is carried from the ear, being located at the thorax, to a defined neuropil in the ventro-lateral protocerebrum of the brain. Thus, the accessibility of the moth auditory pathway combined with its connection to escape responses makes this arrangement well suited for exploring how the nervous system forms a basis for adaptive behaviour.

**TALK 14**

Fri 11.00–11.20

**Animal foraging and the evolution of attentional control**

Thomas Hills (thomhills@gmail.com)

*University of Warwick*

What is attention and what are its evolutionary origins? Foraging and feeding-related behaviours across eumetazoans share similar molecular mechanisms and behavioural phenomenology with fronto-striatal circuits in human goal-directed behaviour. These mechanisms involve dopamine and glutamate in the modulation of behavioural perseveration. These can be characterised as mediating the exploration-exploitation trade-off found in area-restricted foraging, suggesting its early evolution near the origin of eumetazoans. Similar mechanisms in the vertebrate basal ganglia control motor behaviour and cognition and reveal an evolutionary progression toward

increasing internal connections between prefrontal cortex and striatum in moving from amphibian to primate. In addition, the basal ganglia in higher vertebrates show the ability to transfer dopaminergic activity from unconditioned stimuli to conditioned stimuli. The evolutionary role of dopamine in the modulation of goal-directed behaviour and cognition is further supported by pathologies of human goal-directed cognition, which have motor and cognitive dysfunction and organise themselves, with respect to dopaminergic activity, along the exploitation-exploration gradient, from perseverative to unfocused. The evidence strongly supports the evolution of goal-directed cognition out of mechanisms initially in control of spatial foraging, but through increasing cortical connections eventually came to be used to forage for information.

**TALK 15**

Fri 11.20–11.40

**Foraging challenges in statistically structured environments give rise to learning mechanisms which may account for 'advanced cognitive abilities'**

Oren Kolodny (orenkolodny@gmail.com)

*Tel Aviv University*

with Shimon Edelman &amp; Arnon Lotem

To study the evolution of advanced cognitive abilities from simple principles, we developed and implemented a model that uses basic elements of associative learning, but can be modified incrementally to facilitate unsupervised learning of complex environmental regularities. The program receives strings of data as input, and constructs a weighted network that represents associations of items in time and space. It can also segment data sequences, assess their statistical significance, and cluster them hierarchically. Using agent-based simulations of foraging for food, we show that construction of hierarchies, or chunking, may be highly advantageous in environments in which meaningful units are composed of multiple primitive elements. Based on empirical insights from animal and human learning, we propose two separate data acquisition mechanisms for constructing hierarchies and demonstrate how their parameters can be fine-tuned by natural selection to fit the statistical regularities of different environments. Finally, the same model implementation was successfully applied to a set of language learning tasks, suggesting that some of the critical elements required for 'advanced cognitive abilities' could have evolved within the general context of animal foraging in statistically structured environments.

**TALK 16** **Fri 11.40–12.00****From artificial selection to transcriptomics: the cognitive benefits of, and the gene responsible for, a large brain**

Alexander Kotrschal

(alexander.kotrschal@ebc.uu.se)

Uppsala University

University of Veterinary Medicine Vienna

with Peter W. Harrison, Yu-Chia Chen, Pertti Panula,

Judith Mank &amp; Niclas Kolm

The large variation in brain size that exists in the animal kingdom is thought to evolve through the balance between selective advantages of greater cognitive ability and the prohibitively high energy demands of a larger brain. However, support for the trade-off between cognitive ability and energetic costs is based exclusively on correlative evidence and the genetic architecture underlying brain-size evolution remains enigmatic. We used artificial selection for large and small brain size relative to body size in the guppy (*Poecilia reticulata*), and found that relative brain size evolved rapidly in response to divergent selection. After two generations of selection large- and small-brained fish showed numerous behavioural differences such as that large-brained fish outperformed small-brained fish in several tests of cognitive ability. Moreover, large-brained lines developed smaller guts and produced fewer offspring. We then used RNAseq to analyze the transcriptome of the forebrain of those fish and identified a single brain size candidate gene. Because experimental down-regulation of this gene in zebrafish embryos produced a small-brained phenotype we suggest that differences in the candidate gene expression underlie brain size and cognitive differences in vertebrates.

**TALK 17** **Fri 12.00–12.20****What mechanisms underlie visually guided navigation in foraging wood ants (*Formica rufa*)?**

Joseph L. Woodgate (j.l.woodgate@sussex.ac.uk)

University of Sussex

with David D Lent, Paul Graham &amp; Thomas S. Collett

Many animals, including solitary foraging ants, learn visually guided routes between important locations. Despite ants' small brains and low resolution visual system, they can accurately and robustly learn routes of 100m or more. What perceptual, computational and behavioural mechanisms underlie such abilities? We use high spatial and temporal-resolution recordings of wood ants' paths over short routes in the laboratory to identify the mechanisms by which ants control their paths within familiar and transformed scenes. A significant component of directional control involves predictive, saccade-like turns which are driven by learnt visual features of the scene (Lent et al. 2010, PNAS 107, 16348–16353). Ants are capable of a range of perceptual operations that contribute to the visual control of saccade-like turns, such

as placing visual features in a particular location on the retina, calculating the ratio of visual 'mass' on left and right visual fields and segmenting panoramic scenes (Lent et al. 2013, *Curr. Biol.* 23, 684–690). Ants navigate successfully both in open environments, in which visual cues are mostly derived from a distant panorama, and in cluttered environments where salient visual features are close by. We explore the ways in which different perceptual mechanisms are used to drive ants' paths in these different surroundings.

**TALK 18** **Fri 14.00–14.20****The costs of courtship: using physiology and performance to understand what females want**

Sophie L. Mowles

(sophie.mowles@nottingham.ac.uk)

University of Nottingham

Males typically attempt to convince females to mate by performing displays that demonstrate some aspect of their quality. While some displays are elaborate and spectacular in appearance, others involve simple repetitive actions. Dynamic repeated displays may advertise a signaller's stamina, which may be informative in mate choice as it communicates (i) the general health and energy reserves of the signaller or (ii) its ability to perform well in other ecologically relevant activities. Here, I describe a combination of physiological and whole-organism performance indicators that can reveal the relevance of stamina to courtship. For example, courting male field crickets, *Gryllus bimaculatus*, experience heightened levels of haemolymph lactic acid indicative of anaerobic respiration, and the wing-raising courtship display of the Cuban burrowing cockroach, *Byrsotria fumigata*, significantly handicaps its stamina on a racetrack in performance capacity trials. Thus, simple repetitive courtship actions are informative in providing females with information about a male's stamina, allowing females to select physically fit, good-quality mates.

**TALK 19** **Fri 14.20–14.40****The evolution of muscle physiology and social behaviour in Caribbean *Anolis* lizards**

Michele A. Johnson (michele.johnson@trinity.edu)

Trinity University

Lizards in genus *Anolis* (anoles) are a model system in studies of evolution, ecology, and behaviour, yet relatively little is known regarding the diversity of behavioural mechanisms in this group. While the mechanisms associated with social display and copulatory behaviours have been described in the green anole (*A. carolinensis*), we do not yet understand how the physiological and neuroendocrine traits that underlie these behaviours vary across the genus. Using 6–9 species, I used phylogenetically informed comparative analyses to determine whether the frequency of muscle use in display or copulation is associated with the size of the muscle fibres, the fibre type composition of the

muscles, and the expression of androgen receptors in the muscles. Results of these studies reveal that the size of the muscle fibres controlling push-up displays and copulation behaviours are associated with the frequency of their use; but in the muscles controlling dewlap (i.e., throat fan) extensions, expression of androgen receptors is associated with the frequency of dewlap use. Comparing these results to studies of intraspecific variation in the green anole demonstrates that the evolution of behavioural mechanisms across the genus may follow multiple trajectories.

**NIKO TINBERGEN LECTURE**

Fri 14.40–15.40

**The role of behaviour in the establishment of novel traits**

Marlene Zuk (mzuk@umn.edu)

*University of Minnesota*

How do new traits arise, and how are they maintained? All variation ultimately stems from mutation, but while mutations arise continuously, few become established. Of those that do, some may even become widespread very quickly if circumstances allow so-called rapid or contemporary evolution. What distinguishes traits that persist from those that disappear? Novel traits do not arise in a vacuum—they occur in a milieu of other characteristics that may hinder or facilitate their establishment. Using data from recent rapid evolution in crickets, lizards and other taxa, we suggest that novel traits, particularly those important in social evolution or sexual selection, are unlikely to become established unless they can be reinforced by associated behaviours. For example, a mutation rendering male crickets unable to call became established in populations where an acoustically orienting parasitoid fly made silence adaptive. But the crickets were only able to overcome the associated cost to mating success because the acoustic environment during maturation already influenced mating behaviour and allowed the novel morph to attract mates. Behaviour may thus play an important role in the rate of evolution.

**TALK 20**

Fri 16.10–16.30

**Evolution of learning and levels of selection: a lesson from avian parent–offspring communication**

Arnon Lotem (lotem@post.tau.ac.il)

*Tel Aviv University*

with Inbar Biran-Yoeli

In recent years, it has become increasingly clear that the evolution of behaviour may be better understood as the evolution of the learning mechanisms that produce it. However, this approach has rarely been applied to the social and communicative behaviours that are likely to operate in complex social environments and be subject to multi-level selection. We used genetic, agent-based evolutionary simulations to explore how learning mechanisms may evolve to adjust the level of nestling

begging, and to examine the possible consequences of this process for parent-offspring conflict and communication. The results confirm several previous theoretical predictions and demonstrate three novel phenomena. First, negatively frequency-dependent group-level selection can generate a stable polymorphism of learning strategies and parental responses. Second, while conventional reinforcement learning models fail to cope with family dynamics at the nest, a newly developed learning model (that is consistent with recent experimental results) evolved successfully. Third, while kin-selection affected the frequency of the different learning genes, its impact on begging intensity was unexpectedly negligible, demonstrating that evolution is a complex process, and showing that the effect of kin-selection on behaviours that are shaped by learning may not be predicted by simple application of Hamilton's rule.

**TALK 21**

Fri 16.30–16.50

**Socially induced plasticity of sickness behaviours and its neuroendocrine basis**

Patricia C. Lopes (patricia.lopes@ieu.uzh.ch)

*University of Zurich**University of California, Berkeley*

Animals suffering from an infection frequently exhibit symptoms that manifest as reductions in activity, food and water intake, libido and social interactions. While adoption of these “sickness behaviours” may increase the chances of survival by reallocating metabolic resources to fight infection, they may also decrease chances for other adaptive opportunities, such as reproduction. I have exploited this trade-off idea by examining how different social contexts are able to modulate the expression of sickness behaviours in male zebra finches and the associated changes for the neuroendocrine and immune system. My results suggest that sickness behaviours are plastic and male birds are able to alter expression of these behaviours according to their social surroundings, appearing to prioritise the opportunity for current reproductive investment over recovery from infection.

**TALK 22**

Fri 16.50–17.10

**Complex interactions between individual and social learning processes shape their evolution**

Michal Arbilly (ma72@st-andrews.ac.uk)

*University of St Andrews*

with Kevin N. Laland, Uzi Motro, Marcus W. Feldman &amp; Arnon Lotem

Individual and social learning both have their advantages over the other, and their alternative use is thought to be shaped by environmental as well as social conditions. Studies looking into their evolution often assume that learning provides the adaptive solution to any task, and disregard the learning process and its potential difficulties. In a pair of studies, we explicitly modelled individual and social learning in an environment where the highest paying patches are associated with the lowest

probability of obtaining food. On average, these patches are the best foraging option, but when sampling them learners face repeated failures and are likely to avoid revisiting them due to risk aversion, thus requiring a long sampling period to develop a preference for these patches. We found that (1) social learning allows learners to circumvent risk aversion and renders personal experience useless, if not harmful; (2) when considering different types of learning mechanisms (e.g. learning about location and learning about stimulus), tradeoffs between the quality of individual and social information give rise to different combinations of mechanisms. Our results suggest that biases and complications arising from both individual and social learning processes interact to shape the evolution of these two learning alternatives.

TALK 23

Fri 17.10–17.30

### Socially driven changes in neural plasticity mediate behavioural flexibility

Magda C. Teles (mteles@ispa.pt)

ISPA – Instituto Universitário

with Rui F. Oliveira

In social species animals tend to adjust their social behaviour according to the available social information in the group. This changing environment requires for neuronal plasticity of the neural network underlying social behaviour. Two major neural mechanisms have been proposed to mediate these changes, biochemical switching and structural reorganisation of the neural circuits underlying social behaviour that ultimately depend on social regulation of gene expression. In the current work we examine both mechanisms with particular focus on monoamines and neuropeptides as major candidates to mediate biochemical changes, adult neurogenesis as a proxy for rewiring of the networks, and candidate genes (*bdnf* and *npas4*, *wnt3* and *neuroD* and *ngln1*, *ngln2*) to identify different neurogenomic states. For this purpose we used zebrafish (*Danio rerio*) males to study the effects of acute social interactions in rapid changes in the brain. A behavioural paradigm under which male zebrafish consistently express fighting behaviour was used to investigate the effects of different social experiences: winning the interaction, losing the interaction, or fighting an unsolved interaction (mirror image). Our results indicate that different social experiences operate at different levels to promote distinct internal states leading to different behavioural responses. This study will establish the quantitative response of neuronal plasticity in the brain of zebrafish to social changes.

TALK 24

Fri 17.30–17.50

### Non-social learning in a social context

Luc-Alain Giraldeau (giraldeau.luc-alain@uqam.ca)

Université du Québec à Montréal

A plethora of studies explore learning in isolated animals and many others look at social learning in groups. So we know lots about social learning in social animals, asocial

learning in single individuals but very little about the dynamics of non-social learning in animals that live in groups. Knowing that groups often create frequency-dependent situations that change payoffs obtained from alternative behaviours, the question arises whether all group members can or should learn? Here I reinterpret some of my published simulation results that suggest that learning may not be optimal for all members of a group. Then I look at experimental results obtained from a recent published study suggesting the existence of fixed and flexible individuals that change roles according to the foraging game in which they are involved. Taken together, the results imply that learning could be an economic decision rather than an ability that animals have or not. It is perhaps time for an optimal cognition theory: a body of economic models of decisions concerning cognitive processes.

## POSTERS

### POSTER 1

#### Evidence of multiple cognitive systems underlying numerical abilities of vertebrates

Christian Agrillo (christian.agrillo@unipd.it)

University of Padova

with Maria Elena Miletto Petrazzini & Angelo Bisazza

The ability to process numerical information is adaptive in many ecological contexts. Laboratory and field studies support the existence of rudimentary numerical abilities in mammals, birds and fish but there is currently a debate whether a single numerical system or multiple cognitive systems are responsible for these abilities. Using examples from our recent work on poeciliid fish (guppies and mosquitofish), we examine evidence in favour of these two alternatives. When solving classical discrimination tests, fish tend to use the perceptual continuous cues that co-vary with number (e.g. total area occupied by stimuli or density) but if the access to these cues is prevented, fish use pure numerical information just as easily. Integration of different types of information allows greater accuracy than using just one cue. Several lines of evidence suggest that, as in humans, small ( $\leq 4$ ) and large numbers are processed by different systems, an accurate object-tracking system and an approximate number system, respectively. Finally, ontogenetic studies evidenced different developmental trajectories for the ability to discriminate number of shoal mates and number of inanimate objects. We suggest the existence of multiple quantification systems which are domain-specific and serve to solve a limited set of problems.

### POSTER 2

#### Environmental and genetic control of brain and song structure in the zebra finch

Stefan Leitner (leitner@orn.mpg.de)

Max Planck Institute for Ornithology

with Joseph L. Woodgate, Katherine L. Buchanan, Andrew T. D. Bennett, Clive K. Catchpole & Roswitha Brighton

Birdsong is a classic example of a learned trait with cultural inheritance, with selection acting on trait expression. To understand how song responds to selection, it is vital to determine the extent to which variation in song learning and neuroanatomy is attributable to genetic variation, environmental conditions, or their interactions. Using a partial cross fostering design with an experimental stressor, we quantified the heritability of song structure and key brain nuclei in the song control system of the zebra finch and the genotype-by-environment (G\*E) interactions. Neuroanatomy and song structure both showed low levels of heritability and are unlikely to be under selection as indicators of genetic quality. HVC, in particular, was almost entirely under environmental control. G\*E interaction was important for brain development and

[tinyurl.com/winterasab2013](http://tinyurl.com/winterasab2013)

may provide a mechanism by which additive genetic variation is maintained, which in turn may promote sexual selection through female choice. Our study suggests that selection may act on the genes determining vocal learning, rather than directly on the underlying neuroanatomy, and emphasises the fundamental importance of environmental conditions for vocal learning and neural development in songbirds.

### POSTER 3

#### Environmental enrichment promotes neural plasticity and cognitive ability in fish

Anne Gro Vea Salvanes (anne.salvanes@bio.uib.no)

University of Bergen

with Olav Moberg, Lars O. E. Ebbesson, Tom Ole Nilsen, Knut Helge Jensen & Victoria A. Braithwaite

Different kinds of experience during early life can play a significant role in the development of an animal's behavioural phenotype. In natural contexts this influences behaviours from anti-predator responses to navigation abilities. In contrast, for animals reared in captive environments, the homogeneous nature of their experience tends to reduce behavioural flexibility. Studies with cage-reared rodents indicate that captivity often compromises neural development and neural plasticity. Such neural and behavioural deficits can be problematic if captive bred animals are being reared with the intention of releasing them as part of a conservation strategy. Over the last decade there has been growing interest in the use of environmental enrichment to promote behavioural flexibility in animals that are bred for release. Here we describe the positive effects of environmental enrichment on neural plasticity and cognition in juvenile Atlantic salmon (*Salmo salar*). Exposing fish to enriched conditions up-regulated the forebrain expression of NeuroD1 mRNA and improved learning ability assessed in a spatial task. The addition of enrichment to the captive environment thus promotes neural and behavioural changes that are likely to promote behavioural flexibility and improve post-release survival.

### POSTER 4

#### Costly responses to acoustic stressors: underlying physiology, psychology and flexibility?

Julia Purser (julia.purser@bristol.ac.uk)

University of Bristol

with Stephen D. Simpson, Irene Voellmy, Rick Brintjies & Andrew N. Radford

In a resource-limited environment, there is a premium on efficient acquisition of energy and allocation to the various life processes. However, with human activities altering the environment at an unprecedented rate, and vast numbers of animals regularly encountering stress in captivity, animals are faced with conflicting demands to maintain and invest in life processes (and thus potentially contribute to population dynamics) versus respond to

environmental disturbances. Using controlled laboratory experiments with a variety of fish species, we show that the addition of acoustic noise to an otherwise quiet environment has the potential to act as a costly stressor. Examining physiological measures as well as behaviour in a variety of testing scenarios, we see increases in metabolic rate, as well as behaviour typical of stress responses (measures associated with anxiety or fear in classic models: erratic swimming, tank-diving, freezing) and effects on attention (distraction or cognitive bias: startling to previously ignored stimuli, foraging errors). Since such costly effects would be expected to limit potential productivity if repeated over chronic or repeated exposures, we also investigate if the responses are flexible, changing during ongoing or repeated exposures.

#### POSTER 5

### Mood–emotion interaction effects on behavioural and brain reactions of sheep exposed to video images of social interactions

Lorenz Gygax (lorenz.gygax@agroscope.admin.ch)

Agroscope Reckenholz–Tänikon Research Station, Etenhausen

with Sabine Vögeli & Beat Wechsler

Long-term mood has the potential to modulate short-term emotional reactions. We kept two groups of sheep under unpredictable, stimulus-poor or predictable, stimulus-rich conditions for several months. Twenty-four sheep were tested in a cognitive bias paradigm and were exposed to silent video images of group mates showing agonistic interactions (negative), ruminating while lying (intermediate), or feeding tolerantly from one bucket (positive valence). Their behaviour, ear positions and frontal brain reaction were measured. We found weak evidence for a more negative cognitive bias in sheep from the unpredictable group. With respect to valence of the social stimuli, sheep were less likely to direct the head towards the video images with more positive stimuli. The sheep from the predictable group were generally less prone to direct the head towards the stimulus pictures, were less active, and showed a lower proportion of backwards ears irrespective of valence. Frontal brain activity was reduced in sheep from the predictable group if the stimulus was negative. Social stimuli were discriminated by the sheep judged by their head orientation when exposed to the video images. Reactions were hardly modulated by housing conditions although general differences between housing conditions were observed that are attributable to differences in mood.

#### POSTER 6

### The role of dopaminergic system in the modulation of the Indo-Pacific bluestreak cleaner wrasse *Labroides dimidiatus* cooperative behaviour

João P. Messias (jpmiguelmessias@gmail.com)

ISPA – Instituto Universitário

with José R. Paula, Alexandra Grutter, Rui Oliveira, Redouan Bshary & Marta C. Soares

The cleaner wrasse *Labroides dimidiatus* system is considered to be a classic example of mutualism, in which interspecific interactions often yield positive payoffs for all involved parties. Although much is known on the behaviour of this species, its physiological counterpart is less comprehended. The cleaner wrasse *Labroides dimidiatus* is a highly specialized fish species that interacts with all sorts of other reef fish, which requires a great deal of behavioural flexibility. Here we asked if dopamine, a neurotransmitter involved in a variety of behavioural modulating actions that is tied with reward-related learning and decision-making systems, may be a good modulator candidate of these cleaners' behaviour. We tested if the administration of exogenous agonists (SKF38393, Quinpirole) and antagonists (SCH23390, Metoclopramide) would produce any changes in their motivation to interact with other fish. To our knowledge, our study is the first to link the effects of dopamine actions and mechanisms to cooperative behaviour, to which we expect have tremendous effects on the output behaviour of these highly social fish.

#### POSTER 7

### Behavioural and molecular responses to a social challenge in a cooperative breeder reared in different social environments

Cecilia Wikström (cecilia.wikstroem@iee.unibe.ch)

University of Bern

with Stefan Fischer, Nadia Aubin-Horth & Barbara Taborsky

Social competence, the ability to optimize the social behaviour based on social information, can increase the Darwinian fitness of animals. This ability is known to be shaped by early social experience, but the molecular mechanisms driving this developmental variation are largely unexplored. We tested how juveniles of the cooperatively breeding cichlid *Neolamprologus pulcher* reared in different social environments cope with a social challenge, and how brain gene expression relates to rearing environment and social behaviour. Juveniles were reared for two months either with or without a breeder pair and a helper. Subsequently, juveniles of both rearing conditions were either exposed to an asymmetric contest over a resource, or a control treatment without social interactions. Directly afterwards fish of challenge and control treatments were sacrificed to study brain gene expression (GE). We compared (i) the expression of social behaviour between fish reared with or without older

conspecifics and (ii) the expression levels of 8 genes between fish of different rearing conditions and fish exposed to challenge or control treatments. The candidate genes code for hormones and receptors known to be important determinants of social behaviour. GE was measured in the hypothalamus and telencephalon, two key brain areas important for social behaviour.

#### POSTER 8

### Behavioural and genomic responses of a cooperatively breeding cichlid to a helping task

Claudia Kasper (claudia.kasper@iee.unibe.ch)

University of Bern

with Nadia Aubin-Horth & Barbara Taborsky

Understanding the evolution of cooperative behaviour requires both understanding its adaptive function and the underlying mechanisms of behavioural control. The mechanisms driving alloparental brood care in cooperatively breeding fish are largely unexplored. We tested how helpers of the cooperatively breeding cichlid *Neolamprologus pulcher* adjust their amount of alloparental care in response to the social environment (group size) and perceived need of help (egg predation risk) experienced during early life, and how brain gene expression relates both to the early rearing environment and to the expressed helping behaviour. After the rearing phase, young were tested for their helping propensity and their brains were sampled subsequently. The expression of the immediate early gene *egr-1* was used as indicator of genomic activation by the helping task. We compared *egr-1* expression between fish reared in environments with different group sizes and with different need of help. We related the levels of expressed helping behaviour of these treatment groups to their *egr-1* expression in five brain areas to identify the key candidate brain regions where transcriptional cascades controlling the expression of helping behaviour are started.

#### POSTER 9

### Nestmate recognition in Stenogastrinae wasps: visual and chemical information are not integrated in a multimodal sensory cue

David Baracchi (d.baracchi@qmul.ac.uk)

Università degli Studi di Firenze

with I. Petrocelli, G. Ricciardi & S. Turillazzi

Social insects have evolved a highly developed recognition system enabling them to accept nestmates but reject alien conspecifics. So far, chemical communication is assumed to have played a major role in this ability. However this paradigm has recently been challenged by the discovery of visual communication in social wasps. In the primitively eusocial wasp *Liostenogaster flavolineata*, individuals differ in their cuticular hydrocarbons profiles (CHCs) according to their colony membership and each female also possesses

unique facial markings. Here we reveal that although *L. flavolineata* females are able to discriminate between alien and nestmate females using only visual or CHCs cues, these chemical profiles become redundant when the visual and chemical stimuli are presented together. These findings indicate that resident wasps regulate the level of aggression towards other individuals based on facial markings alone. A selective attention process may explain why visual stimuli are dominant over odour stimuli when both cues are available. This is the first report that shows visual channels prevail over odour pathways in a nestmate recognition context. Furthermore our findings suggest that the existence of a cognitive ability demonstrated in an experimental paradigm does not necessarily imply that it is used by the owner in a natural context.

#### POSTER 10

### Sex-specific response to the familiarity of mates, and the role of olfaction

Cedric K. W. Tan (cedric.tan@zoo.ox.ac.uk)

University of Oxford

with Hanne Løvlie, Elisabeth Greenway, Stephen F. Goodwin, Tommaso Pizzari and Stuart Wigby

Studies of mating preferences have largely neglected the behavioural response and mechanism used by individuals encountering their previous mates ('directly familiar'), or new mates that share similarities to previous mates, e.g. from the same family and/or environment ('phenotypically familiar'). Here, we show that male and female *Drosophila melanogaster* respond to the direct and phenotypic familiarity of potential mates in different ways. In the first experiment, we exposed a single focal male or female to two potential partners, one novel (not previously encountered) and one directly familiar (their previous mate). In the second experiment, one potential partner was novel (unrelated, and from a different environment from the previous mate) and one was phenotypically familiar (from the same family and environment as the previous mate). We found that males preferentially courted novel females over directly or phenotypically familiar females. In contrast, females displayed a weak preference for directly and phenotypically familiar males over novel males. Sex-specific responses to the familiarity of potential mates were significantly weaker or absent in *Orc1* mutants, which lack a co-receptor essential for olfaction. Collectively, our results show that direct and phenotypic sexual familiarity is detected through olfactory cues, which play an important role in sex-specific sexual behaviour.

**POSTER 11****Mass spectrometric study of the peptidergic neurotransmission regulating male mating in a mollusc, *Lymnaea stagnalis***

Zineb El Filali (zineb.el.filali@falw.vu.nl)

Vrije Universiteit (VU) Amsterdam

with Anne Bruinen, Gert Eijkel, Joris M. Koene, Ron Heeren &amp; Ka Wan Li

In many animals, copulation behaviour is a complex behaviour consisting of a series of specific movements and decisions that reflect an accurate communication between the male and female partner. This complexity is increased in simultaneous hermaphrodites, such as the great pond snail *Lymnaea stagnalis*, that can choose to mate as male and/or female. All these behaviours and decisions are under the control of a rather simple central nervous system, characterized by a finite number of large, individually identifiable neurons. The latter makes the pond snail an excellent model organism for single cell analysis studies. In order to visualize the neuronal network that regulates the male behaviour, the penial nerve, which innervates the peripheral reproductive organs, was back-filled with a heavy metal (nickel coupled to lysine) to stain neurons that are involved in the coordination of the movements needed during copulation. Those neurons can be divided in 2 categories: (i) Clustered cells, forming the whole anterior and ventral lobe of the right cerebral ganglion and the I-cluster of the right pedal ganglion. (ii) Dispersed cells on the right pleural and parietal ganglia. Earlier studies have revealed the identity and function of neuropeptides in the clustered neurons, but neuropeptide contents of the dispersed cells remain largely unknown. By using a multifaceted mass spectrometric strategy that combines profiling and imaging techniques, we aim to both localise and chemically identify the neuropeptides involved in the regulation of male copulation behaviour in *L. stagnalis*. Ultimately, we expect this to lead to a complete picture of the neural network, and the involved neuropeptides, regulating male behaviour in this hermaphrodite. This can then serve as a basis for exploring how this interacts with the regulation of female reproduction, and how this enables this hermaphrodite to switch between its sexual roles.

**POSTER 12****Scramble competition severely impairs mate choosiness**

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University of Burgundy

with Thomas Brom &amp; Frank Cézilly

Most models of sexual selection rely on the implicit assumption that the individuals can freely compare and spot the best partners in a heterogeneous population. Comparatively, few studies have investigated consequences of the process of mate sampling. Several

sampling strategies have been studied from a theoretical or experimental perspective. They belong to two families of decision rules: best-of- $n$  strategies (individual samples  $n$  partners before choosing the best one among this pool) or threshold strategies (individual sequentially samples available partners and chooses the first one whose quality exceeds a threshold). Almost all models studying such strategies neglect the effect of scramble competition. If, once paired, an individual is removed from the population of available partners, the distribution of partner quality is strongly dependent on the strategies of the other competitors. By means of simple simulations, we show that scramble competition and lost opportunity costs severely impair the evolution of choosy decision rules. In most cases, the evolutionarily stable strategy is to have very low acceptance threshold or to sample at most two individuals in the population. This result may explain some discrepancies between previous model predictions and their experimental validations. It emphasizes the urgent need for considering the pairing process in sexual selection.

**POSTER 13****What makes a forager leave a resource patch? Confronting models with reality**

Thomas S. Hoffmeister (tsh@uni-bremen.de)

University of Bremen

with Eric Wajnberg, Patrick Coquillard, Andra Thiel &amp; Jennifer Uhlig

Imagine an animal searching for patchily distributed resources. At what point in time should the forager decide to leave the patch and search for another patch? And what information may it use for its decision? Most heuristics developed combine the response to events like encounters with resources with the motivational status of the forager. Yet, the behaviours that keep the foragers in the patch or drive them off the patch remain elusive. We developed individual based optimization models that optimize movement patterns for foragers searching for patchily distributed resources, such that they optimize patch residence times. The tendency to remain on the patch is driven by changes along a gradient from exploitative to explorative movement patterns that are a function of search time, resource encounters and resource distribution. We confront these models with data from parasitoids foraging for hosts that are either dispersed or aggregated across patches and test whether changes in movement patterns predicted by theory are found in live animals.

**POSTER 14****Heritable personality traits probably aren't correct Bayesian priors**

Benja Fallenstein (benja.fallenstein@gmail.com)

University of Bristol

We expect that animals in areas with fewer predators will tend to be bolder, because genes for boldness will have been more successful in previous generations: bold

animals behave as if they expect fewer predators in their environment, and they turn out to be quite correct! Perhaps at an evolutionarily stable equilibrium, an animal's genes will endow it with a Bayesian prior that accurately reflects the range of environments experienced by individuals with the same genotype? Unfortunately, not so. The problem is that offspring in safer areas are more valuable to an allele for boldness than to an allele for shyness, because the first allele's offspring do better there (and vice versa for more dangerous areas). This means that in order to be stable against mutations at the polymorphic locus, the alleles would have to influence not only the animal's prior, but also the quantity it is trying to maximize. But then, a mutation pushing the animal towards simply maximizing ordinary reproductive success would be able to invade at a different locus, a case of intragenomic conflict (Leimar et al., 2006). Hence, there is no evolutionarily stable equilibrium, and little reason to expect optimality in either sense.

**POSTER 15****Active search and self-experience mediate the success of both social and individual learning in house sparrow fledglings**

Noa Truskanov (noatrs@gmail.com)

Tel Aviv University  
with Arnon Lotem

In some birds, joining conspecifics and scrounging on their food findings may block learning of food related cues, thus hindering social learning. Here we show, however, that hand-raised house sparrow fledglings that are imprinted on a mother model and scrounge on her food findings, can readily learn to use the sand colour chosen by the mother as a cue for the presence of food during independent foraging. Our results also demonstrate that such social learning may indeed be less effective when it is not mediated by self-learning: Fledglings who followed a mother that pointed to the location of the seeds, coercing them to dig actively in the sand, developed a significantly stronger preference than fledglings whose mother exposed the seeds for them. A step-by-step analysis of the learning process suggests that fledglings gave more weight to successes that resulted from active search than from finding seeds exposed by the mother. Further experiments extend these findings to the context of individual learning, showing that given a choice between two colours associated with the same payoff, fledglings prefer the colour associated with active search over the colour associated with exposed seeds.

**POSTER 16****Behavioural flexibility and learning in orb spiders**

Thomas Hesselberg

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University of Oxford

Spider webs and their detailed geometry constitute an ideal system in which to study the flexibility and learning of foraging behaviour in a small-brained invertebrate. A large number of studies show that whereas spiders do not seem to improve the basic design of their webs with age, size or experience, they do modify their webs in response to previous prey catching experiences. They furthermore show an impressive flexibility in their ability to adapt their orb webs to windy conditions, leg loss, lack of gravity and constrained space. In this presentation I will primarily focus on behavioural flexibility of web-building behaviour in the latter and demonstrate how different species differ in their ability to adapt their webs to vertical and horizontal frames. Equally interesting I will show how the acacia orb spider *Eustala illicita* immediately adapts its first web to the available space, but shows no improvement in subsequent webs. I will discuss this apparent lack of learning and compare it to orb spiders' response to less frequently occurring phenomena such as leg loss and lack of gravity.

**POSTER 17****Learning by observing others arises through simple associations in an insect model**

Erika H. Dawson (e.h.dawson@qmul.ac.uk)

Queen Mary University of London

with Aurore Avargues-Weber, Lars Chittka &amp; Ellouise Leadbeater

Recent debate has questioned whether animal social learning truly deserves the label "social". Solitary animals can sometimes learn from conspecifics, and social learning abilities often correlate with individual learning abilities, so there may be little reason to view the underlying learning processes as adaptively specialized. Here, we demonstrate how learning by observation may arise through a simple Pavlovian ability to integrate two learned associations in a bumblebee model system. Bumblebees are known to learn how to recognize rewarding flower colours by watching conspecifics from a distance, and we found that previous associations between conspecifics and reward are critical to this process. We place a complex social learning phenomenon within a simple Pavlovian framework that is common to social and solitary species alike.

**POSTER 18****Not so simple associative learning**

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Associative learning is often discussed as a simple alternative that should be ruled out before positing a

cognitive or representational explanation of animal behaviour. Yet many current accounts of associative learning assume it involves acquisition of knowledge about contingencies, and explicit internal prediction to guide behavioural choices, which are surely cognitive capacities. Could such representational mechanisms exist even in small-brained animals, such as insects? Or have qualitatively distinct mechanisms for associative learning evolved? I will discuss intersecting behavioural, neurobiological and modelling data relevant to these issues.

**POSTER 19****Internal state modulation of visual motion processing in walking blowflies**

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with Holger G. Krapp

Locomotion alters the neural basis of visual motion processing in a diverse range of animals including mice, rats, zebra fish, locust and flies. It is not clear whether these changes are linked to changes in the dynamics of the visual input that accompany behaviour, or changes in the animal's internal state, such as locomotor speed or metabolic status. To address these questions we recorded the activity of visual interneurons in blowflies walking on a trackball. We found that walking increases the resting activity and sensitivity to high velocities at different levels of motion adaptation. This modulation was dependent on the walking speed and not on the extent of motion adaptation. In addition, we found that food deprivation reduced the modulation, such that after three days without food, locomotion no longer significantly modulated the responses. Thus it appears that internal states of the animal, the locomotor speed and metabolic status, influence how walking modulates visual processing. We are now investigating the consequences of these neural changes for optomotor visual stabilisation reflexes which these neurons mediate.

**POSTER 20****Locusts show handedness during goal-orientated movements**

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with Jeremy E. Niven

Handedness in limb control has been well-documented across a wide range of vertebrate taxa, including humans. Many of these studies have linked handedness to asymmetries in the nervous system known as lateralisation. In contrast to vertebrates, there has been relatively little research on handedness in invertebrates. We investigated whether desert locusts (*Schistocerca gregaria*) show a preference for using a particular forelimb whilst crossing a gap in the substrate upon which they are walking. Locusts must use their forelimbs to reach across the gap and make contact with the opposite side. We found that locusts exhibit a leg

preference when crossing the gap. This preference varies among individuals; some prefer to use their right forelimb, others their left. We compared the preference for a particular limb with controls in which the gap was either removed or replaced by a clear plastic surface. We also recorded leg movements before the initiation of gap crossing to determine whether an individual's preference was the product of a decision making process or simply a continuation of the walking pattern. These results show that small insect nervous systems, which lack pronounced lateralisation, are capable of generating handedness in limb control. The results also shed light into the evolution of handedness in limb control, which was previously thought only to exist in vertebrates.